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Preface

Mangrove ecology – applications in forestry and costal zone management

> "In Persia in the Carmanian district, where the tide is felt, there are trees [Rhizophora mucronata] . . . [that] are all eaten away up to the middle by the sea and are held up by their roots, so that they look like a cuttle-fish"
>
> Theophrastus (370–285 B.C.E.), *Enquiry into Plants* IV. VII. 5
> (Translated by Sir Arthur Holt, 1916)

Mangrove forests have entranced and intrigued naturalists, botanists, zoologists, and ecologists for millennia. Over two thousand years ago, Theophrastus published perhaps the first explanation of why the roots of these trees grow aboveground and how they grow in brackish and salty water, and he also observed that their viviparous seeds sprouted while they are still within the fruits attached to the branches. Straddling the land and sea, mangroves provide natural resources of both; wood for lumber and fuel, and fish and prawns for protein. They are home to resident and migratory birds, snakes, and mammals, and simultaneously support incredible diversity and biomass of crabs, sponges, tunicates, and other benthic marine invertebrates. Mangroves absorb nutrients and sediments flowing down rivers from uplands through estuaries, and they offer protection to these uplands and estuaries from battering waves and cyclonic storms. In this new millennium, we must ask if the diversity of mangroves and the many ecosystem functions they provide can be retained and sustained when mangrove forests continue to be cut to provide logs for charcoal kilns and wood chips for rayon mills, drained to construct commercial aquaculture operations, filled with garbage, and "reclaimed" for coastal developments.

The twelve papers in this special issue of *Aquatic Botany* on the ecology of mangrove forests provide comprehensive reviews of the fundamental knowledge that literally thousands of scientists have accumulated over hundreds of years that can be used to answer these pressing questions. The papers range widely and represent many scientific disciplines: paleontology, population biology, ecosystem ecology, economics, and sociology, to name just a few. By providing summaries and syntheses of existing data, the 54 authors and co-authors of these papers set the benchmarks and foundations on which future studies will build. Perhaps more importantly, these reviews illustrate clearly that for addressing many issues that are central to the conservation, management, and preservation of mangrove ecosystems, there is more than enough data to make informed decisions and to guide sensible actions.

Between one and two percent of the world's mangrove forests are being lost to chainsaws, prawn and crab ponds, and new settlements, condominiums, and waterfront resorts each year. This rate of destruction is comparable to the annual rate at which upland tropical forests are being cut, burned, and converted to pastures, farms, towns, and cities. Declarations from regular conferences organized by academics, individual governments, regional interest groups, non-governmental organizations, and the United Nations routinely decry the loss of mangroves, but often encourage more research before the needed actions can be reliably implemented. Although the dozen papers in this issue identify gaps in our knowledge, these papers clearly show that those gaps are small relative to the vast amounts of information available to policy analysts, decision makers, and managers. The data are here, well organized and clearly presented. Use these data wisely: the time for action is now.

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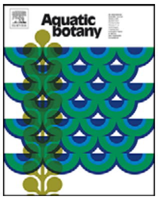

Personal report

Aquatic Botany special issue dedication to Samuel Curry Snedaker (22 May 1938–21 March 2005)

This special issue of *Aquatic Botany* is inspired on the well-known UNESCO publication by Snedaker and Snedaker (1984). More than a decade has passed since another major issue on the biodiversity and function of mangrove ecosystems has been published (Field and Whittaker, 1998). The contacts for publishing the present special issue were established on a series of Australian mangrove and wetland conferences and workshops in 2006. Our aim was to provide a series of comprehensive reviews on mangrove ecology, in particular on applications in forestry and coastal zone management. We highlight the existence of a parallel special issue focusing more on macrobenthic fauna from mangroves (Lee and Dittmann, 2008). Finally, we refer to Aaron Ellison's preface to this *Aquatic Botany* Special Issue on 'Mangrove ecology—applications in forestry and coastal zone management' for a state-of-the-art of mangrove ecosystems (Ellison, 2008), before coming back to the inspiration by and dedication to a great man.

In this dedication we want to express our respect to the late Sam Snedaker with a few anecdotes:

Al Ain, United Arab Emirates, December 1996. *I still cannot believe Nico sent me to my first international conference abroad as a starting PhD student. Have you seen the program? Snedaker, Duke, Saenger, Lee, Field, Ball, Popp,. . . what on Earth am I going to present to thése people? Thé Snedaker is going to be there!* But then came the announcement of my presentation . . ..

Immediately after that I was confronted with Sam's charisma. He calmly came towards me and made me feel as if I were one of the big names on that program. He gave me so much confidence during the talks we had that I was convinced there was a mangrove future out there.

Miami, Florida, September 1999. Coming back from the New Orleans conference of the Estuarine Research Foundation there was only one stop to make for us before crossing the Atlantic again, and that was Sam's office in Miami and the New World mangroves nearby. The most remarkable sight that is burnt in our minds is *Avicennia germinans* cut like a hedge on the nearby golf course, and the most remarkable remembrance of Sam was his hospitality when he invited us into his small office.

With the courtesy of Rafael J. Araujo we use some of the beautiful words with which he described Sam, which is exactly how we remember him and how we feel about him.

> "I always wanted to know how Sam felt about this legacy. Was he proud of it? Did it open doors for him? – He would look at me and say nothing. You see, there was a detachment about Sam, a mystery about him that unsettled many. Sam was especially good at concentrating large thoughts into a little space, at getting to the heart of things, and at preserving valuable information. His words were few, but carried weight. I loved him for all he knew, taught me and said; but also for his silence. I miss his quiet entry into the office, his unobtrusiveness, his sense of privacy and calm. . ."

Sam, this mangrove issue of *Aquatic Botany* is in your memory. A memory that we will keep alive, and a memory that makes us realise to whom this poem of mine was destined:

When you watch the ocean we were given,
And look at how the waves are driven,
Towards any tropical coast,
Towards a forest, towards a host.
Towards a ground made for breeding,
Where one is lodged or comes for feeding,
Where the water meets the land,
Where you only find this plant.

Once a seedling must have stranded,
Making this site so enchanted,
Lots of creeks, lots of roots,
Lots of curious floating fruits.
Unusual systems for dispersing,
Exotic life forms there for nursing,
Swimming, jumping, climbing trees,
Fish and crabs and more of these.

Many threats is what they face,
Try surviving their own ways,
All subjected to hard stress,
But still thriving nonetheless,
What on Earth is this unlike ?
Which plant is forming a living dyke ?
Who is it rooting in the sea ?
The mangrove tree,
The mangrove tree.
FDG

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References

Araujo, R.J., 2005. Samuel Curry Snedaker (1938–2005). Bull. Mar. Sci. 76, 623–624.

Ellison, A.M., 2008. Preface. Preface. Aquat. Bot. 89, 77.

Field, C.B., Whittaker, R.J., 1998. Biodiversity and function of mangrove ecosystems. Glob. Ecol. Biogeog. Let. 7, 1–94.

Lee, S.Y., Dittmann, S., 2008. Preface. J. Sea Res. 59, 1–11.

Snedaker, S.C., Snedaker, J.G., 1984. The Mangrove Ecosystem: Research Methods. UNESCO, Paris.

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Review

Long-term retrospection on mangrove development using transdisciplinary approaches: A review

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ABSTRACT

Large ecosystem processes often take place beyond the observation time of a researcher. Yet, through retrospective research scientists can approach and understand ecosystem changes. This contributes to the fundamental understanding of both human-induced and natural dynamics in ecosystems worldwide. This also holds for fast changing coastal areas with mangrove ecosystems, which are important for biodiversity, for coastal protection, and for the daily livelihood of millions of people in tropical coastal developing countries. In addition, retrospective research generates a basis for predictions that can be used early on to protect an ecosystem. In attempting to protect ecosystems from adverse human-induced change and destruction, and to manage them for sustainability, scientists are only beginning to investigate and understand natural ecosystem dynamics. It is important and advisable to gather, combine and analyse all possible data that allow a researcher to look back in time. This paper reviews the available retrospective methods, and highlights the transdisciplinary way (i.e. combination between basic and applied sciences on one hand, and social and human sciences on the other) in which retrospective research on a scale between months and centuries can be carried out, but it also includes methods on larger scales that may be marginally relevant. The paper particularly emphasizes the lack of transdisciplinary (not interdisciplinary) integration between sciences in retrospective research on mangrove forests in the past.

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1. Introduction

Mangrove forests occur along tropical and subtropical coastlines and serve as breeding, spawning, hatching, and nursery grounds for many marine species (Baran, 1999; Barbier, 2000; Nagelkerken et al., 2008; Cannicci et al., 2008). Next to this habitat function, mangroves also provide wood and non-wood forest products and values to indigenous people (Bandaranayake, 1998; Ewel et al., 1998; Gilbert and Janssen, 1998; Rönnbäck, 1999; Bandaranayake, 2002; Moberg and Rönnbäck, 2003; Walters et al., 2008). They may act as a physical barrier to protect human settlements from the ocean (Badola and Hussain, 2005; Dahdouh-Guebas et al., 2005c; Danielsen et al., 2005; Dahdouh-Guebas and Koedam, 2006). It has been estimated that approximately 75% of tropical coasts world-wide were once fringed with mangroves (Chapman, 1976), but at present a world without mangroves is no longer an unrealistic prospect (Duke et al., 2007). Despite their values, mangroves are amongst the most threatened ecosystems world-wide, subject to over-exploitation, pollution, and conversion (Farnsworth and Ellison, 1997). In particular the large-scale conversion of mangrove forests to ponds for shrimp aquaculture is an underestimated problem (Naylor et al., 2000a,b; Dahdouh-Guebas et al., 2002b; Primavera, 2005). Not only direct or destructive anthropogenic effects such as clear felling, but also indirect impacts such as changes in hydrography have proved detrimental to mangroves (Dahdouh-Guebas et al., 2005b,c). In addition, climate change poses a threat to mangrove ecosystems (Gilman et al., 2008). This has stimulated many countries to pay attention to natural or induced mangrove recovery (Stevenson et al., 1999; Lewis et al., 2005; Bosire et al., 2008). In many locations, the above-mentioned threats have reduced the potential for economic recovery. For instance, economic recovery from the 26/12/2004 tsunami disaster is hampered because of the loss of traditional income sources related to coastal ecosystems rich in species and in ecological functions (Adger et al., 2005; Hughes et al., 2005). To reverse the eroding social-ecological resilience in mangrove areas under threat, it is important to reconstruct the past of the mangrove ecosystem, or better: the mangrove anthroposystem. This reconstruction is also the basis to understand its natural and anthropogenic dynamics (Berger et al., 2008), to forecast changes, and strive for early mitigation.

Few have attempted to forecast general impacts (Semeniuk, 1994; Clarke, 1995; Ellison and Farnsworth, 1996; Woodroffe, 1999), and even fewer to predict cryptic changes in more specific ecosystem characteristics such as vegetation structure and composition (Dahdouh-Guebas and Koedam, 2002; Dahdouh-Guebas et al., 2002a, 2005a). These studies have pointed out that there is a lack of description and understanding of past changes, and present functions and processes, let alone the ability to predict future scenarios in mangrove ecosystems. The need for long-term environmental monitoring, research and paleoecological reconstructions of past environments has been stressed (Parr et al., 2003). Historical ecology data have been adopted in the past in this perspective. Swetnam et al. (1999) state that 'historical ecology encompasses all of the data, techniques, and perspectives derived from paleoecology, land use history from archival and documentary research, and long-term ecological research from monitoring and experiments extending over decades. Also included are time series from instrument-based observations of the environment, such as weather records, stream gauges, and data from satellites'. However, the 'natural' and 'documentary archives' that contribute to historical ecology are with few exceptions from within natural sciences (Swetnam et al., 1999) overlooking highly valuable information derived from the social and human sciences (Cormier-Salem, 1999; Rist and Dahdouh-Guebas, 2006). This is corroborated by the significant lack of integration between disciplines from various science domains, particularly in historical research applied to mangrove forests. The term 'retrospective research' is used here to indicate all research approaches that look back in time to understand the present (historical ecology, historical biogeography, etc. . .).

The objective of this review paper is to highlight the potential of retrospective research on mangroves, and to recommend transdisciplinary approaches based on a subset of retrospective research methods to improve our understanding of past changes and spatio-temporal dynamics on a scale between months and centuries. In this light, transdisciplinarity equals interdisciplinarity that transcends the science fields (basic and applied science; social and human science; life science) in particular, and science in general (incorporating indigenous forms of knowledge) (Rist and Dahdouh-Guebas, 2006).

2. Retrospective data from the basic and applied sciences

2.1. Above-ground fieldwork observations

Measurements or visual observations in the field can be indicative for events in the recent past, such as tracks or broken branches for animal foraging, or concentrations of aromatic hydrocarbons for pollution (Burns et al., 1993; MacFarlane et al., 2003). Ecosystem morphology and physiognomy can provide a range of information on the past. The position and physiognomy of mangrove forests and coral reefs reflect changes on different time scales. Transient surface water levels (reflected in flood line marks on the vegetation) and shoreline position respond most rapidly to coastal environmental changes, and can be reflected in changes in colour, structure and mud coatings of stems and branches of plants, notches in channel banks, aggregated surfaces of wetlands, and more geomorphologic indicators (Morton, 2002). Distributional changes such as the natural expansion or regression of mangrove vegetation (including possible changes in species composition) and coral reefs are indicators of environmental changes occurring on the order of decades to millennia (Morton, 2002; Dahdouh-Guebas et al., 2004). Past exploitation practices can be deduced from the age structure and spatial distribution of trees (Dahdouh-Guebas et al., 2002a), the straightness of trees (Kairo et al., 2002), or the presence of tree stumps or dead trees (Dahdouh-Guebas et al., 2004). The difficulty with most of the above observations is that the time scale of reconstruction is very variable, and cannot always be quantified based on the observation alone (what is the time interval for a change to occur or to be observable?).

2.2. Lichenometry

Based on the radial, slow and steady growth of most lichens, lichenometry is commonly used as a technique to date the exposure of certain natural or human features, such as bridges, gravestones, landslides or geological features (Bull and Brandon, 1998; Winchester and Chaujar, 2002). However, the assessment of lichens in forest gap dynamics (Benson and Coxson, 2002) also opens doors to lichenometry in a mangrove forest ecosystem context. Lichens do occur in mangroves (e.g. Ellison, 1997), but are not well studied, let alone used in lichenometry.

2.3. Dendrochronology

Dendrochronology is the science of measuring time-related features in the wood of woody plants. As woody plants grow, tree cambium produces xylem at the pith side of a root, stem or branch section, which may display variable characteristics depending on seasons or environmental conditions. Seasonal climates of the temperate type induce the formation of rings in the xylem of a tree. Dendrochronologic research can be purely based on the wood-anatomical characteristics of these tree rings that must be analysed visually or through image analysis (Cherubini et al., 2003), or it can be based on the analysis of isotopes extracted from the successive tree rings (February, 2000). However, both approaches are obscured in areas where the spatio-temporal climatic variability inhibits tree rings to form consistently such as under mediterranean or tropical climates (Cherubini et al., 2003). Nevertheless, for the mangrove trees rings have demonstrated to be useful for age determination (Menezes et al., 2003; Verheyden et al., 2004a), with potential for dendrochemistry (Verheyden et al., 2004b, 2005a) and for research on wood anatomy and hydraulic architecture (Schmitz et al., 2006). Growth layers of *Avicennia* are not annual which is, however, related to their peculiar growth via successive cambia (Schmitz et al., 2007a,b). Some other mangrove species do show growth rings in regions with a seasonal climate. In *Rhizophora mucronata* Lamk., annual growth rings were identified in Kenya (Verheyden et al., 2004a,b) and also *Heritiera fomes* Buch.-Ham and *Sonneratia apetala* Buch.-Ham from Bangladesh show a good potential for dendrochronological research (Chowdhury et al., in press).

Following the above approach, environmental and ecological aspects of a system can be deduced from the characteristics of the tree rings. Dendroecology may reveal changes in for instance fire incidence (Stephens et al., 2003), climatic conditions (Briffa et al., 1998; Verheyden et al., 2005b), total environments or ecosystems (February, 2000), sea-level rise (Yu et al., 2004) and even retrospective information on fish abundance hidden in the rings of riparian trees (Drake et al., 2002). Normally the natural archiving of information, which can be used in dendrochronology, stops when a tree dies, and it is therefore important to know how long ago a tree died. To solve this, methods have been proposed to estimate the time a dead tree has been on the ground (Gore et al., 1985; Johnson and Greene, 1991).

2.4. Landscape (repeat) photography

Landscape photography from a single location is often used to view the typical landscape features under different environmental conditions such as seasons in temperate regions, or inundation in fluvial or tidal forests (Stafford-Deitsch, 1996). Such comparative photographs have also been used to compare the ‘before’ and ‘after’ situations in case of catastrophes or successive stages in restoration studies (Lewis, 1982; Finn, 1996; Turner and Lewis, 1997; Stevenson et al., 1999). However, apart from documentary books for a wide audience (Vanhecke et al., 1981), few scientists used sequential photographs to actually research ecosystem or vegetation changes (e.g. Rogers et al., 1984; Butler and DeChano, 2001; Brook and Bowman, 2006; Moseley, 2006), or to corroborate other data (e.g. Wolanski and Gereta, 2001). Although the analysis of such sequential photographs is often limited to visual inspection, the inherent information to interpret ecosystem changes in a wide framework can be very valuable (Fig. 1). Landscape photography or repeat photography definitely qualifies as a cheap and accessible data source for the present and future, but for the past it evidently requires reference photographs.

Fig. 1. Repeat landscape photography of a selected mangrove stand in Gazi Bay (Kenya) from approximately the same place taken in 1993 (top) and in 2003 (bottom). Over a period of 10 years, the unaffected *Sonneratia alba* J. Smith stand on the background is thriving, but the cleared mangrove area on the foreground has failed to recover naturally from the over-exploitation, necessitating rehabilitation (cf. Bosire et al., 2008).

2.5. Air- and space-borne remote sensing

One of the most widely used methods to look into the recent past, and which will undoubtedly evolve into the single most important monitoring technology in the future, is remote sensing. There is a large difference between air- and space-borne remote sensing as far as their spatial, temporal and spectral characteristics are concerned (Green et al., 2000; Dahdouh-Guebas, 2002). Whereas satellite remote sensing is a relatively new technology that started with the Apollo program in 1963, the first black/white aerial photographs were taken in 1858 from a hot air balloon, and in 1906 from an airplane. It was during World War I that aerial photography missions on a large scale were launched. Hence, aerial photography constitutes the only available imagery for retrospective monitoring on a sequential scale of decades, starting long before the birth of space technology (Dahdouh-Guebas et al., 2000b). Aerial photography remains the only imagery with the highest spatial resolution, and is often preferred to satellite imagery (Ramsey and Laine, 1997; Mumby et al., 1999; Hyyppä et al., 2000; Manson et al., 2001; Thampanya et al., 2006). Of course, the choice of a particular sensor depends on the study purpose (cf. Blasco et al., 1998).

From as recently as 2001, images of very high spatial resolution and of good spectral resolution from space-borne sensors (Ikonos, Quickbird, OrbView) have made it possible to optimise the identification of differential assemblages, genera and species within and beyond mangrove ecosystems (Wang et al., 2004; Dahdouh-Guebas et al., 2005a; Kovacs et al., 2005). Before that, the application of satellite sensors in change detection was limited to large homogeneous land-cover or land-use classes. The research community should consider also the ‘physiognomic resolution’ of remote sensing methods or of any method. The ‘physiognomic resolution’ is referred to as the form that a method is able to identify within the variety of life forms, or as the ecological entity that a method is able to identify within an ecosystem (e.g. forest, individual). It implies that the identified level can be monitored to detect temporal changes in it. For instance, a method (e.g. a sensor) that is able to make physiognomic distinctions such as ‘grassland’, ‘forest’, ‘submerged vegetation’, even if fitted with further characterisations like ‘dense’ and ‘sparse’, would be considered having a ‘low physiognomic resolution’. So would a method that can only detect whether an ecosystem entity is mangrove forest or not, without further details. However, a method that succeeds in identifying the taxonomic level of *species* or even individuals would be considered having a very high physiognomic resolution. Studies that serve to pinpoint individual trees will require methods with a very high physiognomic resolution.

Next to spatial resolution of remote sensing sensors and physiognomic resolution, the very high temporal resolution of satellite remote sensing (as frequent as 3 days to revisit a particular place) is conducive for the detection of changes on small temporal intervals. The higher radiometric resolution is also an advantage. Unfortunately, the highly commercialised cost poses a restriction on its use by institutions in developing countries.

2.6. Isotope analyses

Isotope analysis may employ the use of ‘radiogenic isotopes’ or ‘stable isotopes’. Radiogenic isotopes are not stable and undergo radioactive decay that can be traced back in time by comparing the mass of the original element to that of the element newly formed during the decay process. Based on the time that is required for a certain mass of an original radiogenic isotope to spontaneously decay to half of its mass (=the isotope’s half-life), it may have a specific medical or environmental application on a time scale between seconds and billions of years (Firestone and Shirley, 1996). Radiocarbon (^{14}C) for instance, has a half-life of 5700 years and is widely used for long-term dating in ecosystem research including mangroves (Scheel-Ybert, 2000; Lezine et al., 2002). However, its use in the reconstruction of a specific vegetation type may be limited due to its low ‘floristic resolution’ (Witt, 2002). Nevertheless, even when the time scale focused on is at most centuries, radiocarbon dating remains interesting to know how long the mangrove ecosystem under study has already been in its current place. Alternative radiogenic isotopes for the study of more recent sedimentation are ^{137}Cs (half life = ±30 years), ^{210}Pb (half life = ±22 years) and ^{7}Be (half life = ±53 days) (Lynch et al., 1989; Blake et al., 1999, 2002). We refer to J.C. Ellison (2008) who details the dating techniques and methods for long-term retrospection on mangrove development using sediment cores.

In contrast, stable isotope analysis is based on ratio’s between heavy isotopes that do not decay (e.g. ^{13}C, ^{15}N) and the lighter isotopes (e.g. ^{12}C, ^{14}N). In ecology, stable isotopes are used to trace the cycling or fixation of nutrients such as in research on trophic relationships between organisms and between adjacent ecosystems (Marguillier et al., 1997; Bouillon et al., 2002, 2003; Cocheret de la Morinière et al., 2003; Bouillon et al., 2007; Kristensen et al., 2008). For instance, diet shifts in herbivorous marine animals, detected through stable isotope analysis of specimens caught on different moments, may be an indicator for a changed supply in primary food sources. Isotope analysis can also be applied to dendrochronological research to investigate past environmental factors that are perpetuated in the tree rings under the form of stable or unstable radiogenic isotopes (February, 2000; Miller et al., 2006). Isotopes in microfossils originating from marine sediments may reveal temperature, salinity, ice volume, atmospheric CO_2, and ocean circulation (Stokstad, 2001).

2.7. Substrate cores

Centimeter- to meter-deep soil cores can provide significant insight in past conditions, on a scale from years to millions of years. Apart from indications of soil consolidation or compaction based on the structural and textural characteristics of the soil, research foci can range from biogeochemical trace elements or isotopes (Bouillon et al., 2002; Gonneea et al., 2004; Versteegh et al., 2004), over palynology (Blasco, 1984; Lezine, 1996; Hofmann, 2002; Yulianto et al., 2004; Vedel et al., 2006; A.M. Ellison, 2008; J.C. Ellison, 2008) and species compositions in general (Westgate, 1994), to climatic changes and sea-level rise (Verschuren et al., 2000; Kumaran et al., 2004a,b; Cohen et al., 2005a,b; Torrescano and Islebe, 2006; Engelhart et al., 2007).

The use of substrate cores is however not limited to surface soils, and offers most interesting insights when applied to underwater substrates (Wang et al., 1999; Verschuren et al., 2000). Substrate coring also extends to the study of ice cores that can be well over a hundred meters deep and look back into the climate ten to hundred thousands of years (e.g. Thompson et al., 1998). For both methods the results may incorporating a wide area including mangrove ecosystems that are located relatively near mountains with ice caps or glaciers in tropical regions, or near great lakes. The cost and technology of extraction, preservation and analysis often poses a practical limitation to the study of deep soil or ice cores, in particular for below-surface substrates.

A third form of ‘substrate’ cores is the analysis of corals, which grow slowly and accumulate information on a seasonal time scale. The study of corals may reveal sea surface temperature from oxygen isotopes and elemental ratios, and river discharge and precipitation cycles on land from isotopes (Stokstad, 2001). This also allows the study of oceanic or climatic impacts or consequences of global change, such as sea-level rise (or decrease), ocean surges (e.g. tsunamis), and El-Niño events. Once more, this is a method that is primarily carried out nearby, but not in the mangrove. Yet, many mangrove forests (e.g. in Kenya) are known to host ancient coral reefs.

2.8. Geomorphological and paleontological data

Deltaic-estuarine geomorphology influences the development of mangrove forests. Various settings along which mangroves develop have been identified and described, and include protected shores, bays, estuaries, deltas and river banks (Thom et al., 1975; Thom, 1984). Mud stains and microbial etching on exposed rocks, notches in wave-cut scarps and anomalous landforms often indicate changed environments. In Kenya for example, the presence of coral pillars within the mangrove (e.g. Gazi Bay), in the back mangrove (e.g. Wasini Island), or buried under inhabited terrestrial villages (e.g. Mida Creek), are unambiguous indicators of a former sea-level that used to be at least 10 m higher than at present (Farid Dahdouh-Guebas, unpublished data, 2003), which can have an oceanological cause (sea-level change) or a geological one (tectonics), or a combination.

Next to this type of direct relationships, unlinked paleontological studies can provide elements from the distant past that can help interpret mangrove ecosystem origin or changes. Tephrochronological studies have for instance been applied to date tropical coastal environments (Ward and Little, 2000; Morton, 2002). The study of fossils indicate biogeographical shifts in faunal or floral assemblages (Smith et al., 2001), that may also be interpreted into an ecosystem context.

2.9. Hereditary and evolutionary feature differentiation

The differentiation of hereditary information between populations of a particular species is a measure for the frequency of contact between them, in the form of diaspores (pollen, seeds or entire individuals). This can be viewed over a series of spatial scales, between a few thousand square meters and intercontinental surfaces, and temporal scales, between months and millennia (Gaston, 1996; Triest, 2008). For some species, genetic differentiation may reflect habitat fragmentation, isolation or degradation (Abeysinghe et al., 2000; Gaston, 1996; Triest, 2008). However, this is largely dependent on the biology of the species. Anemogamous-hydrochorous species will evidently not display the same pattern of differentiation as entomogamous-autochorous species.

The analysis of hereditary information based on morphological characteristics or on DNA is also at the basis of phylogeny research, which can be used to date an organism (Roelants and Bossuyt, 2005). Kinship between organisms and evolutionary features can in turn reflect geographical and environmental changes, such as tectonics or sea level (Lin et al., 2002; Bossuyt et al., 2004). However, such results reflect more on the biological species rather than on the site in which they are found. Dating a particular habitat in a certain location through phylogeny of its associated fauna is only possible if the animals are endemic to that site.

3. Retrospective data from the social and human sciences

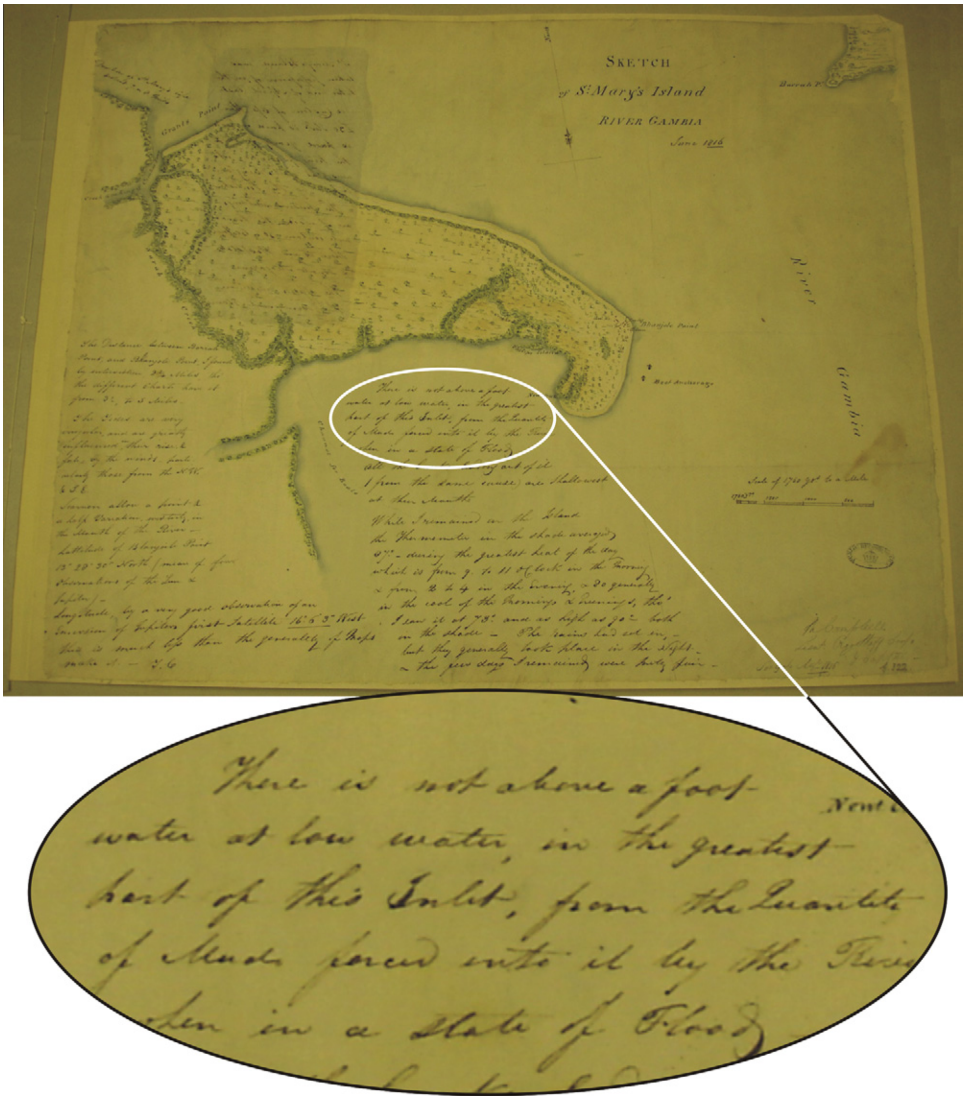
3.1. Interviews

The information that resides with indigenous people, and in particular with the elders of local communities, is vast and extremely valuable and can easily be accessed through interviews. It is also extremely vulnerable, as information is rapidly lost with their passing away. Western scientific knowledge has long been blind to indigenous forms of knowledge, even though the latter has much to offer for bio-cultural diversity and sustainable resource use (Rist and Dahdouh-Guebas, 2006). Ethnobotanical surveys for instance can reveal a great deal about past and current plant–man relationships (Kovacs, 2000; Dahdouh-Guebas et al., 2000a; Hernández-Cornejo et al., 2005; Walters, 2005; Dahdouh-Guebas et al., 2006; Walters et al., 2008). It can be expanded to surveys on fishery-related or ethnozoological practices and thus reveal general ecosystem changes through time. In addition, interview surveys can be soundly combined with retrospective remote sensing, as ground truthing past imagery is not possible. Simple information such as the ability to wash clothes with lagoon water, as opposed to 30 years earlier, are invaluable sociological indicators for a low lagoon water salinity (Jayatissa et al., 2002; Dahdouh-Guebas et al., 2005b). In another example the origin of a cleared patch of vegetation in Gazi (Kenya) was clarified with local informants' knowledge (Dahdouh-Guebas et al., 2004). Interview analyses have also been used in studying physical, rather than biological, aspects of the natural environment, such as in ethnopedology (WinklerPrins and Sandor, 2003).

3.2. Historic archives

Historic archives are often used in history, archaeology or within other disciplines of the social and human sciences (e.g. Lape, 2002). Countries that used to have overseas territories (such as France, Portugal, Spain, The Netherlands and the United Kingdom) usually keep colonial archives. The Atlas of Mutual Heritage for instance (http://www.atlasofmutualheritage.nl/), which comprises the archives of the Dutch East-India Company (Vereenigde Oost-Indische Compagnie—VOC) and the Dutch West-India Company (West-Indische Compagnie—WIC), contains thousands of plans, maps, views, panoramas, scenes of everyday life, and many more descriptions that can be used as a source of information (e.g. Baldaeus, 1672). Historic expertise is needed to soundly interpret ancient descriptions, or scribbled notions in the margins of 17th century maps (Fig. 2). Sometimes sets of words such as 'till here reaches the sea water and all land is silty' (*tot dusverre komt het zeewater en is alles brak en siltagtig land*), 'drowned land' (*verdroncken landt*) and 'bending rhizophorous belts' (*Deze tweede rhizophorengordel vormt bogten en inhammen en wordt door talrijke smalle straten doorsneden, die veelal de beddingen zijn van op het land ontspringende kreken*, Von Rosenberg, 1867) are unambiguous indications of the presence of a mangrove ecosystem. Probably the oldest known unambiguous references to mangroves going on for several paragraphs read amongst others: *In Persia in the Carmanian district, where the tide is felt, there are trees* [*Rhizophora mucronata*]...[that] *are all eaten away up to the middle by the sea and are held up by their roots, so that they look like a cuttle-fish* (Theophrastus, 370-285 B.C.E.), as cited by A.M. Ellison (2008) in the preface of Aquatic Botany's Special Issue on Mangrove Ecology (Dahdouh-Guebas and Koedam, 2008). Other clues given by Theophrastus (370–285 B.C.) are: *In the island of Tylos, which is situated in the Arabian gulf, they say that on the east side there is such a number of trees when the tide goes out that they make a regular fence* on the coastal protection function of mangroves (Enquiry into Plants Book IV. VII. 7), and *As for the tall fruit-bearing trees found in tidal waters, one would perhaps not assign their feeding to the sea water, but say that it is possible that the roots draw potable water from the ground, and that the sea water surrounding the tree does it no more injury than the surface waters surrounding freshwater plants* on the salt tolerance of mangroves (De Causis Plantarum Book II. 5.2 1–9).

Despite the valuable information contained in such historic archives, there is no evidence of their utilisation to study any aspect of the essential tropical coastal ecosystems. In fact, there are



There is not above a foot
water at low water, in the greatest
part of this Inlet, from the Quantity
of Mud forced into it by the River
when in a State of Flood

Fig. 2. Map of St. Mary's Island and associated mangrove creeks (drawn by Lieutenant Thomas Campbell, Lt Royal Staff Corps and Captain in Senegal in 1816). The eastern part of the island (Bhanjole Point) is the current location of The Gambia's capital city Banjul. The inset details part of the notes on distances, tides, winds, direction and temperature and is relevant for biological interpretation on mangrove ecosystem dynamics. (Map archive held by the National Archives of the United Kingdom, Kew, England, U.K.: code MPG 1/322).

only 3 peer-reviewed studies listed in Web of Science® (2007) that have attempted to use the archives of the Dutch or English East India Company in a fundamental exact scientific, rather than a historical, social or human scientific context: one incorporating ship logs to study the weather during and after the little ice age (Farrington et al., 1998), one using early chart making to study the evolution of a major delta front (Allison, 1998), and one combining 17th century historic text and map archives with vegetation science, remote sensing, hydrology and socio-economic interviews to infer the dynamics of mangrove lagoons (Dahdouh-Guebas et al., 2005b). In addition, there is one study that uses long-term meteorological observatory records started by the English East India Company to reconstruct atmospheric pressure (Allan et al., 2002). However, the recognition of the archives of the Dutch East-India Company (1602–1800) in UNESCO's Memory of the World Register (Edmondson, 2002; UNESCO, 2003), is indicative of the much larger research potential available using this or other historic archives. Of course, other archives are scattered around the world, but likewise have few studies on mangroves used them (e.g. Alleng, 1998; Plaziat and Augustinus, 2004).

3.3. Spiritual heritage

Archives and heritage of global religions display very little variability, and are in this sense independent from the studied site. However, they can provide insight into the relation between man and environment (Palmer and Finlay, 2003). While they may not directly generate information on a particular ecosystem, faith may provide a framework for the behaviour of people towards nature, and what they are allowed or not allowed to do in this respect. The protection of the forest of Harissa of the Maronite Church in Lebanon for instance, or other examples of sacred forests near monasteries, temples and pagodas, may provide relevant information as to when human impacts on the forest is likely to have ceased or at least diminished (Palmer and Finlay, 2003). Specifically for mangrove forests there are only a few peer-reviewed published papers highlighting local spiritual archives in order to understand the mangrove forest's history. For instance, Kathiresan and Bingham (2001) and Kathiresan (2002) highlight spiritual beliefs associated to *Excoecaria agallocha* L., which is worshipped in the south of India near Chidambaram, and believed to cure leprosy. Certain beliefs or taboos are related to the mangrove in East-Africa as well (e.g. kayas in Kenya). In the Solomon Islands, the bodies of the dead are disposed of and special rites are performed in the mangrove waters (Vannucci, 1997). A last but most fascinating documentation of the spiritual significance of mangroves stems from the *Asmat* communities in Indonesia (see also Walters et al., 2008). According to their legends, the creator of the *Asmat* carved human-like figurines out of a mangrove root, and with the rhythm played on a self-made drum from mangrove wood, these figurines came to life (Mastaller, 1997). Mystic totem poles made from *Rhizophora* wood are still carved by the *Asmat* today (Mastaller, 1997).

3.4. Archaeological and paleoethnobiological data

If present near a study area, archaeological sites can provide elements that can be interpreted in an ecological way. For example, ancient water management practices and people's dependency of and impact on rivers were indicated by archaeological remains nearby (Brohier, 1934; Juleff, 1996; Lezine et al., 2002). Another example is the insight on changes in faunistic assemblages (Keegan et al., 2003) or transgression of mangrove shorelines (Kendrick and Morse, 1990) provided by studying at archaeological excavation sites. In turn, biological information is also known to assist archaeologists, such as in the lichenometric dating of tombs (Winchester and Chaujar, 2002), rock art (Bednarik, 2002), or as in quartz hydration dating (Erickson et al., 2004).

Paleoethnobiological research may provide insight into past pollen records (Coil et al., 2003), biological diversity (Bonzani, 1997), or pre-historic land conversion (Piperno, 1998), all of which are relevant and underexploited in the understanding of changing environments (Lepofsky et al., 2001).

4. Transdisciplinary retrospective approaches

The effort to obtain and analyse archived material can be considerable. It is appropriate to evaluate the added value of such a procedure and these steps. When retrospection is the only means of obtaining information about causes of actual phenomena the added value is obvious. In fact this applies to most environmental issues where either long-term processes take place or where direct experimentation is not possible, or both. Mangroves are a highly dynamic environment in space and time, in which recognizable natural landmarks that are stable over time are few. Historically they were left out of human land development, which renders them underdocumented and quite featureless in terms of human landmarks. Yet, the various approaches presented here have contributed to our understanding of their development. We encourage scientists to share, where possible, transdisciplinary research approaches rather than interdisciplinary ones, because as evidenced in this paper, there is more potential for transdisciplinary studies than what is used today in mangrove research.

Interdisciplinarity within some science domains is obviously not new, as some research fields are commonly used in pairs with others. One example is the calibration of sediment stratigraphy and palynology (or other biotic distributions in the sediment) by dating techniques (Mulrennan and Woodroffe, 1998; Ellison, 1999; Stevenson, 2004; Horton et al., 2005), or dendrochronology calibration by radiocarbon dating (e.g. Biondi and Fessenden, 1999; Stein et al., 2000). Another example are combinatory retrospective approaches such as remote sensing–geobotany–geomorphology (Souza-Filho and El-Robini, 2000; Souza-Filho and Paradella, 2002, 2003), dendrochronology–isotope analysis (February, 2000) or dendrochronology–fish catch data (Drake et al., 2002).

However, the use of transdisciplinarity is a completely different story, and is heavily underexploited, as indicated for instance by the restricted use of historic archives detailed above. The variety of retrospective methods from different disciplines over a wide series of retrospective scales indicates that seldom one cannot look back in time (Fig. 3). Particularly in the light of ecosystem or environmental change innovative combinations are possible (Table 1). That transdisciplinary approaches on mangrove ecosys-

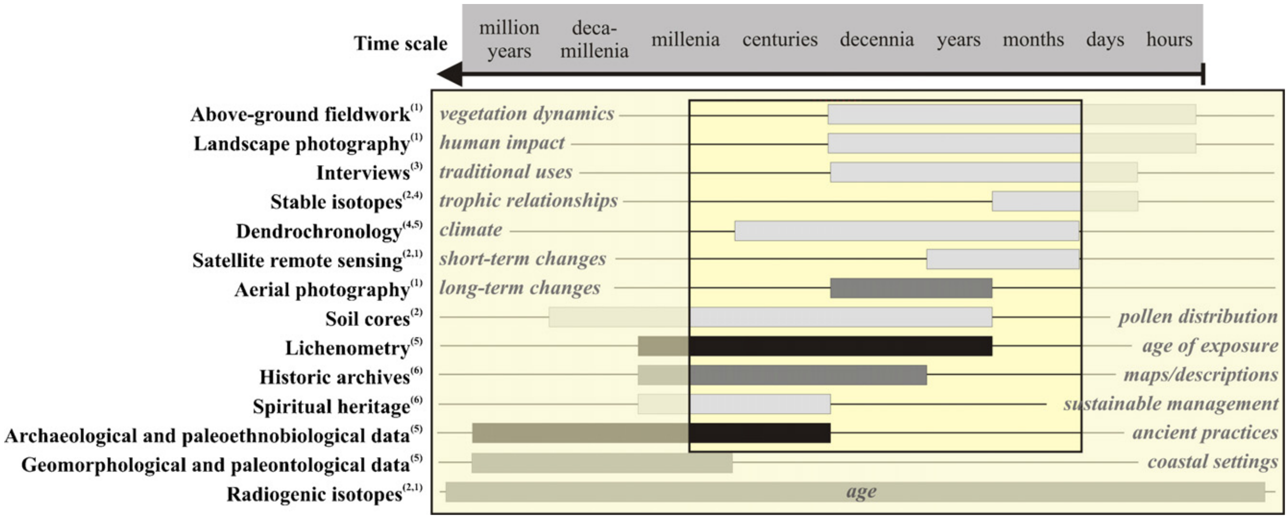


Fig. 3. Data sources for retrospective research, with examples or application fields (grey italics). The temporal scale is not continuous, but functionally classified (between hours and millions of years) with respect to the data sources. The square window represents the most relevant temporal window in the light of mangrove ecosystem change, and illustrates the transdisciplinarity of the data sources over basic, applied, social and human sciences. The degrees of availability of the data sources are indicated using colours—light grey: always available or can be collected; dark grey: is often available but depends on specificities, e.g. although available in most countries, aerial photography may be absent for particular years and sites; black: is much less universal and often not available. Limitations to the data sources that may not be overcome are indicated in superscipt: (1) limited by available data collected in the past such as species lists, imagery of environmental parameters (retroprojection of present fieldwork can mislead and cannot be validated); (2) limited by high cost of extraction, analysis or purchase; (3) limited by people's memory and life time, and by the respondents' reliability and possible bias; (4) limited to biological and chemical assimilation processes; (5) limited by the natural availability of the data; (6) limited by the nature and organisation of the archive database, the type of information displayed and the spatial resolution. For each data source an example of what can be studied is indicated in italic (I refer to the text for detailed explanation and references to scientific literature).

Table 1

Suggestions (based on best professional judgement) of methods and approaches (as ordered and numbered in the text) to be combined, if present, for arbitrarily summarized objectives (in alphabetic order) of studies on mangrove forests

Study objective	2.1. Above-ground observations	2.2. Lichenometry	2.3. Dendrochronology	2.4. Landscape photography	2.5. Aerial photography	2.5. Satellite remote sensing	2.6. Stable isotopes	2.6. Radiogenic isotopes	2.7. Substrate cores	2.8. Geomorphological and paleontological data	2.9. Hereditary and evolutionary feature differentiation	3.1. Interviews	3.2. Historic archives	3.3. Spiritual heritage	3.4. Archaeological data	3.4. Paleoethnobiological data	Number of rated peer-reviewed mangrove studies (Web of Science®) with the respective topic in the title, abstract or keywords (based on the term 'mangrove' plus words from the first column, their synonyms or their wildcards), and that use the added value of retrospection to investigate this topic
Canopy gap dynamics	●	●		●	●	●						●					0 out of 15 (0%)
Changes in fisheries catches	●				●							●					6 out of 17 (35%)
Changes in utilisation patterns (use, wood, non-wood)	●			●								●	●	●	●	●	9 out of 20 (45%)
Dependency of subsistence users	●			●								●	●	●		●	4 out of 5 (80%)
Evaluation of natural tree mortality	●	●	●		●	●		●	●			●					0 out of 8 (0%)
Evaluation of tree logging	●	●			●	●		●				●					4 out of 8 (50%)
Forest management policy	●				●	●						●	●	●			11 out of 22 (50%)
Historic environmental impacts			●		●	●	●	●	●	●		●	●				9 out of 11 (82%)
Natural hazards	●			●	●	●		●	●	●		●	●	●			7 out of 17 (41%)
Past climatic impacts			●				●	●	●	●		●	●	●	●		18 out of 24 (75%)
Phytoremediation	●					●	●	●	●			●					0 out of 4 (0%)
Reafforestation (replanting)	●			●	●	●					●	●					5 out of 13 (39%)
Recent environmental impacts	●					●	●	●	●			●					10 out of 17 (59%)
Sea-level rise or changes	●							●	●	●			●				117 out of 125 (94%)
Vegetation structure: succession	●			●	●	●			●			●					13 out of 20 (65%)

In each case transdisciplinary and retrospection provides an added value for interpretation within the research theme

Table 2
Examples of mangrove and non-mangroves case-studies that adopt transdisciplinary retrospective research approaches thereby creating an added value for insight into a particular study topic

Study topic	Mangrove study and research approaches used	Non-mangrove study and research approaches used
Hydrographical changes	Transitions in ancient inland freshwater resource management using historic text and map archives, vegetation science, remote sensing, hydrology and socio-economic interviews (Dahdouh-Guebas et al., 2005b)	River behaviour and Holocene alluviation (Wales, UK) using archaeological evidence, C-14 dates, terrace mapping, heavy metal analysis, grain size analysis and historical maps (Taylor and Lewin, 1996)
Protection against wind, storms, hurricanes,. . .	Hurricane impacts using vegetation science and interviews in an analytical hierarchy process approach (Kovacs et al., 2004)	Role of scattered vegetation in wind erosion control (northern Burkina Faso) using vegetation science, pedology, erosion modelling and interviews (Leenders et al., 2005; Visser et al., 2005)
Forest management based on vegetation history	Forecasting of future vegetation structure development using on aerial photography, social surveys, and distribution of trees (Dahdouh-Guebas et al., 2004)	Development, distribution, structure and composition of upland forests (Scottish Highlands) and its consideration in management using cultural records, historic maps, vegetation science and geographical information systems (Holl and Smith, 2007)
Shoreline position	Shoreline evolution using historic map archives and remote sensing (Allison, 1998)	Sandy beach evolution (Maine, USA) using side-scan sonar, seismic reflection profiles, ground-penetrating radar, soil cores, historic maps and aerial photographs (Kelley et al., 2005)
Climate change	Adapting to a changing climate using climatology, biological sampling and management (Meynecke, 2005)	Wind speed and navigation using meteorology, climatology and historic text archives (Farrington et al., 1998)

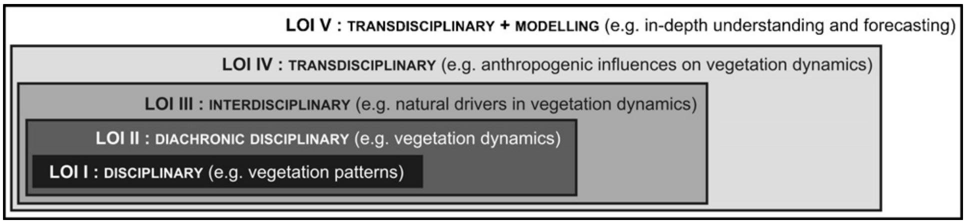


Fig. 4. Levels of insight (LOI) gained with increase of combinatory approaches involving various disciplines from basic and applied as well as from social and human sciences. The ideal situation is that each higher LOI level contains all lower LOI levels. A simple example from vegetation science illustrates that a basic descriptive disciplinary level of insight (LOI), LOI I, may teach us something about contemporary patterns in vegetation. A diachronic approach looking back in time may increase the LOI to II enabling the study of vegetation dynamics. LOI III requires the involvement of another discipline allowing the explanation of natural and anthropogenic factors (through basic and applied sciences) driving vegetation dynamics, whereas LOI IV is gained when information is gained directly from people (using scientific methods from social and human sciences) and their influence on vegetation dynamics. Finally, when all factors are put together and the approach is enriched with a modelling component the LOI increases to V, enabling in-depth understanding and forecasting. Modelling could be applied without ever including socio-ecologic data from local communities, but ideally the higher LOI levels should include all of the lower LOI levels in an attempt to improve insight. See text for specific references illustrating the levels of insight.

tems has or could provide an enhanced insight can be illustrated best by highlighting matches with non-mangroves case-studies that combined data from basic and applied sciences with data from social and human sciences to gain better understanding in certain research topic (Table 2).

As a matter of fact, some combinatory uses of data sources obviously call for the expertise and technology to analyse and interpret them without bias (e.g. historic expertise for ancient archives, see Fig. 2). In other cases data or analyses are very costly or certain other limitations may apply and may pose a restriction on their use (Fig. 3). However, in the majority of cases data sources that are almost always available, and that can always be explored easily and cheaply, are present: above-ground fieldwork observations, interviews, aerial photography, historic and religious archives.

We maintain that the level of disciplinarity used in research is a factor in gaining insight into the functioning of the ecosystem (Fig. 4). The example from vegetation science to illustrate the level of insight (LOI) gained (Fig. 4) can be completed by the following references:

- LOI I: e.g. Triest (2008), Nagelkerken et al. (2008);
- LOI II: e.g. Komiyama et al. (2008);
- LOI III: e.g. Bosire et al. (2008), Cannicci et al. (2008), A.M. Ellison (2008), J.C. Ellison (2008), Gilman et al. (2008), Krauss et al. (2008), Kristensen et al. (2008);
- LOI IV: e.g. Walters et al. (2008);
- LOI V: e.g. Berger et al. (2008).

This overview exemplifies that there is a huge potential for transdisciplinary research (i.e. as defined above) in order to better understand mangrove ecosystems and their dynamics, and although presented for the mangrove habitat here, we maintain it might be valid for a wide range of ecosystems worldwide.

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References

Abeysinghe, P.D., Triest, L., De Greef, B., Koedam, N., Hettiarachchi, S., 2000. Comparative genetical and geographic variation of the mangrove tree *Bruguiera* in Sri Lanka. Aquat. Bot. 67, 131–141.

Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R., Rockström, J., 2005. Social–ecological resilience to coastal disasters. Science 309, 1036–1039.

Allan, R.J., Reason, C.J.C., Carroll, P., Jones, P.D., 2002. A reconstruction of Madras (Chennai) mean sea-level pressure using instrumental records from the late 18th and early 19th centuries. Int. J. Climatol. 22, 1119–1142.

Alleng, G.P., 1998. Historical development of the Port Royal mangrove wetland, Jamaica. J. Coast. Res. 14, 951–959.

Allison, M.A., 1998. Historical changes in the Ganges-Brahmaputra delta front. J. Coast. Res. 14, 1269–1275.

Badola, R., Hussain, S.A., 2005. Valuing ecosystem functions: an empirical study on the storm protection function of Bhitarkanika mangrove ecosystem. India. Environ. Conserv. 32, 85–92.

Baldaeus, P., 1672. Naauwkerige beschryvinge van Malabar en Chromandel, der zelver aangrenzende ryken, en het machtige eyland Ceylon: nevens een omstandige en grondigh doorzochte ontdekking en wederlegginge van de afgodery der Oost-Indische heydenen. Janssonius van Waasberghe, Amsterdam (in ancient Dutch).

Bandaranayake, W.M., 1998. Traditional and medicinal uses of mangroves. Mangroves Salt Marshes 2, 133–148.

Bandaranayake, W.M., 2002. Bioactivities, bioactive compounds and chemical constituents of mangrove plants. Wetlands Ecol. Manage. 10, 421–452.

Baran, E., 1999. A review of quantified relationships between mangroves and coastal resources. Phuket Mar. Biol. Centre Res. Bull. 62, 57–64.

Barbier, E.B., 2000. Valuing the environment as input: review of applications to mangrove-fishery linkages. Ecol. Econ. 35, 47–61.

Bednarik, R.G., 2002. The dating of rock art: a critique. J. Archaeol. Sci. 29, 1213–1233.

Benson, S., Coxson, D.S., 2002. Lichen colonization and gap structure in wet-temperate rainforests of northern interior British Columbia. Bryologist 105, 673–692.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Biondi, F., Fessenden, J.E., 1999. Radiocarbon analysis of *Pinus lagunae* tree rings: Implications for tropical dendrochronology. Radiocarbon 41, 241–249.

Blake, W.H., Walling, D.E., He, Q., 1999. Fallout beryllium-7 as a tracer in soil erosion investigations. Appl. Radiat. Isot. 51, 599–605.

Blake, W.H., Walling, D.E., He, Q., 2002. Using cosmogenic beryllium-7 as a tracer in sediment budget investigations. Geografiska Annaler Ser. A – Phys. Geogr. 84A, 89–102.

Blasco, F., 1984. Mangrove evolution and palynology. In: Snedaker, S.C., Snedaker, J.G. (Eds.), The Mangrove Ecosystem: Research Methods. UNESCO, Paris, pp. 36–49.

Blasco, F., Gauquelin, T., Rasolofoharinoro, M., Denis, J., Aizpuru, M., Caldairou, V., 1998. Recent advances in mangrove studies using remote sensing data. Mar. Freshwater Res. 49, 287–296.

Bonzani, R.M., 1997. Plant diversity in the archaeological record: A means toward defining hunter-gatherer mobility strategies. J. Archaeol. Sci. 24, 1129–1139.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Manamendra-Arachchi, K., Ng, P.K.L., Schneider, C.J., Oommen, O.V., Milinkovitch, M.C., 2004. Local endemism within the Western Ghats–Sri Lanka biodiversity hotspot. Science 306, 479–481.

Bouillon, S., Raman, A.V., Dauby, P., Dehairs, F., 2002. Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). Estuar. Coast. Shelf Sci. 54, 901–913.

Bouillon, S., Dahdouh-Guebas, F., Rao, A.V.V.S., Koedam, N., Dehairs, F., 2003. Sources of organic carbon in mangrove sediments: variability and possible ecological implications. Hydrobiologia 495, 33–39.

Bouillon, S., Connolly, R.M., Lee, S.Y., 2007. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res., doi:10.1016/j.seares.2007.05.001.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Harris, I.C., Shiyatov, S.G., Vaganov, E.A., Grudd, H., 1998. Trees tell of past climates: but are they speaking less clearly today? Philos. Trans. R. Soc. London Ser. B – Biol. Sci. 353, 65–73.

Brohier, R.L., 1934. Ancient Irrigation Works in Ceylon. Ceylon Government Press, Colombo.

Brook, B.W., Bowman, D.M.J.S., 2006. Postcards from the past: charting the landscape-scale conversion of tropical Australian savanna to closed forest during the 20th century. Landscape Ecol. 21, 1253–1266.

Bull, W.B., Brandon, M.T., 1998. Lichen dating of earthquake-generated regional rockfall events, Southern Alps, New Zealand. Geol. Soc. Am. Bull. 110, 60–84.

Burns, K.A., Garrity, S.D., Levings, S.C., 1993. How many years until mangrove ecosystems recover from catastrophic oil spills? Mar. Pollut. Bull. 26, 239–248.

Butler, D.R., DeChano, L.M., 2001. Environmental change in Glacier National Park, Montana: an assessment through repeat photography from fire lookouts. Phys. Geogr. 22, 291–304.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Chapman, V.J., 1976. Mangrove vegetation. J. Cramer, Vaduz.

Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., Innes, J.L., 2003. Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. Biol. Rev. 78, 119–148.

Chowdhury, M.Q., Schmitz, N., Verheyden, A., Sass-Klaassen, U., Koedam, N., Beeckman, H. Nature and periodicity of growth rings in two Bangladeshi mangrove species. IAWA J., in press.

Clarke, P.J., 1995. The population dynamics of the mangrove *Avicennia marina*, demographic synthesis and predictive modelling. Hydrobiologia 295, 83–88.

Cocheret de la Morinière, E., Pollux, B.J.A., Nagelkerken, I., Hemminga, M.A., Huiskes, A.H.L., van der Velde, G., 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. Estuar. Coast. Shelf Sci. 55, 309–321.

Cohen, M.C.L., Behling, H., Lara, R.J., 2005a. Amazonian mangrove dynamics during the last millennium: the relative sea-level and the Little Ice Age. Rev. Palaeobot. Palynol. 136, 93–108.

Cohen, M., Souza Filho, P.W.M., Lara, R., Behling, H., Angulo, R.J., 2005b. A model of Holocene mangrove development and relative sea-level changes on the Bragança Peninsula (northern Brazil). Wetlands Ecol. Manage. 13, 433–443.

Coil, J., Korstanje, M.A., Archer, S., Hastorf, C.A., 2003. Laboratory goals and considerations for multiple microfossil extraction in archaeology. J. Archaeol. Sci. 30, 991–1008.

Cormier-Salem, M.C., 1999. The mangrove: an area to be cleared... for social scientists. Hydrobiologia 413, 135–142.

Dahdouh-Guebas, F., Mathenge, C., Kairo, J.G., Koedam, N., 2000a. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. Econ. Bot. 54, 513–527.

Dahdouh-Guebas, F., Verheyden, A., De Genst, W., Hettiarachchi, S., Koedam, N., 2000b. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. Bull. Mar. Sci. 67, 741–759.

Dahdouh-Guebas, F., 2002. The use of remote sensing and GIS in the sustainable management of tropical coastal ecosystems. Environ. Dev. Sustainability 4, 93–112.

Dahdouh-Guebas, F., Koedam, N., 2002. A synthesis of existent and potential mangrove vegetation structure dynamics from Kenyan, Sri Lankan and Mauritanian case-studies. Meded. Zitt. K. Acad. overzeese Wet./Bull. Séanc. Acad. r. Sci. Outre-Mer 48, 487–511.

Dahdouh-Guebas, F., Kairo, J.G., Jayatissa, L.P., Cannicci, S., Koedam, N., 2002a. An ordination study to view vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka. Plant Ecol. 161, 123–135.

Dahdouh-Guebas, F., Zetterström, T., Rönnbäck, P., Troell, M., Wickramasinghe, A., Koedam, N., 2002b. Recent changes in land-use in the Pambala-Chilaw Lagoon complex (Sri Lanka) investigated using remote sensing and GIS: conservation of mangroves vs. development of shrimp farming. Environ. Dev. Sustainability 4, 185–200.

Dahdouh-Guebas, F., Van Pottelbergh, I., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on retrospective remote sensing, social surveys, and distribution of trees. Mar. Ecol. Prog. Ser. 272, 77–92.

Dahdouh-Guebas, F., Van Hiel, E., Chan, J.C.-W., Jayatissa, L.P., Koedam, N., 2005a. Qualitative distinction of congeneric and introgressive mangrove species in mixed patchy forest assemblages using high spatial resolution remotely sensed imagery (IKONOS). Syst. Biodivers. 2, 113–119.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005b. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., Lo Seen, D., Koedam, N., 2005c. How effective were mangroves as a defence against the recent tsunami? Curr. Biol. 15, R443–R447.

Dahdouh-Guebas, F., Collin, S., Lo Seen, D., Rönnbäck, P., Depommier, D., Ravishankar, T., Koedam, N., 2006. Analysing ethnobotanical and fishery-related importance of mangroves of the East-Godavari Delta (Andhra Pradesh, India) for conservation and management purposes. J. Ethnobiol. Ethnomed. 2, 24.

Dahdouh-Guebas, F., Koedam, N., 2006. Coastal vegetation and the Asian tsunami. Science 311, 37–38.

Dahdouh-Guebas, F., Koedam, N. (Eds.), 2008. Aquatic Botany special issue on Mangrove Ecology – Applications in Forestry and Coastal Zone Management. Aquat. Bot. 89, 77–274.

Danielsen, F., Sørensen, M.K., Olwig, M.F., Selvam, V., Parish, F., Burgess, N.D., Hiraishi, T., Karunagaran, V.M., Rasmussen, M.S., Hansen, L.B., Quarto, A., Suryadiputra, N., 2005. The asian tsunami: a protective role for coastal vegetation. Science 310, 643.

Drake, D.C., Naiman, R.J., Helfield, J.M., 2002. Reconstructing salmon abundance in rivers: an initial dendrochronological evaluation. Ecology 83, 2971–2977.

Duke, N.C., Meynecke, J.-O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Edmondson, R., 2002. Memory of the World: General Guidelines (Revised edition 2002). UNESCO, Paris.

Ellison, A.M., Farnsworth, E.J., 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica 24, 549–565.

Ellison, A.M., 2008. Preface. Aquat. Bot. doi:10.1016/j.aquabot.2008.01.001, this issue.

Ellison, J.C., 1997. Mangrove community characteristics and litter production in Bermuda. In: Kjerfve, B., de Lacerda, L.D., Diop, E.H.S. (Eds.), Mangrove Ecosystem Studies in Latin America and Africa. UNESCO, Paris, pp. 8–17.

Ellison, J.C., 1999. Impacts of sediment burial on mangroves. Mar. Pollut. Bull. 37, 420–426.

Ellison, J.C., 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: A review. Aquat. Bot. 89, 93–104.

Engelhart, S.E., Horton, B.P., Roberts, D.H., Bryant, C.L., Reide Corbett, D., 2007. Mangrove pollen of Indonesia and its suitability as a sea-level indicator. Mar. Geol. 242, 65–81.

Erickson, A.A., Bell, S.S., Dawes, C.J., 2004. Does mangrove leaf chemistry help explain crab herbivory patterns? Biotropica 36 (3), 333–343.

Ewel, K.C., Twilley, R.R., Ong, J.E., 1998. Different kinds of mangrove forests provide different goods and services. Global Ecol. Biogeogr. Lett. 7, 83–94.

Farrington, A.J., Lubker, S., Radok, U., Woodruff, S., 1998. South Atlantic winds and weather during and following the little ice age—a pilot study of English East India Company (EEIC) ship logs. Meteorol. Atmos. Phys. 67, 253–257.

Farnsworth, E.J., Ellison, A.M., 1997. The global conservation status of mangroves. Ambio 26, 328–334.

February, E.C., 2000. Archaeological charcoal and dendrochronology to reconstruct past environments of southern Africa. S. Afr. J. Sci. 96, 111–116.

Finn, M., 1996. The mangrove mesocosm of Biosphere 2: design, establishment and primary results. Ecol. Eng. 6, 21–56.

Firestone, R.B., Shirley, V.S., 1996. Table of Isotopes, 8th edition. John Wiley & Sons Inc., New York.

Gilbert, A.J., Janssen, R., 1998. Use of environmental functions to communicate the values of a mangrove ecosystem under different management regimes. Ecol. Econ. 25, 323–346.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Gaston, K.J., 1996. Biodiversity. A biology of Numbers and Difference. Blackwell Science Ltd., Oxford.

Gonneea, M.E., Paytan, A., Herrera-Silveira, J.A., 2004. Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years. Estuar. Coast. Shelf Sci. 61, 211–227.

Gore, A.P., Johnson, E.A., Lo, H.P., 1985. Estimating the time a dead tree has been on the ground. Ecology 66, 1981–1983.

Green, E.P., Mumby, P.J., Edwards, A.J., Clark, C.D., 2000. Remote sensing handbook for tropical coastal management. Coastal Management Sourcebooks, vol. 3. UNESCO, Paris.

Hernández-Cornejo, R., Koedam, N., Ruiz Luna, A., Troell, M., Dahdouh-Guebas, F., 2005. Remote sensing and ethnobotanical assessment of the mangrove forest changes in the Navachiste-San Ignacio-Macapule lagoon complex, Sinaloa, Mexico. Ecol. Soc. 10, 16.

Hofmann, C.-C., 2002. Pollen distribution in sub-recent sedimentary environments of the Orinoco Delta (Venezuela)—an actuo-palaeobotanical study. Rev. Palaeobot. Palynol. 119, 191–217.

Holl, K., Smith, M., 2007. Scottish upland forests: history lessons for the future. Forest Ecol. Manage. 249, 45–53.

Horton, B.P., Gibbard, P.L., Mile, G.M., Morley, R.J., Purintavaragul, C., Stargardt, J.M., 2005. Holocene sea levels and palaeoenvironments, Malay-Thai Peninsula, southeast Asia. Holocene 15, 1–15.

Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S., Wilson, J., 2005. New paradigms for supporting the resilience of marine ecosystems. Tree 20, 380–386.

Hyyppä, J., Hyyppä, H., Inkinen, M., Engdahl, M., Linko, S., Zhu, Y.H., 2000. Accuracy comparison of various remote sensing data sources in the retrieval of forest stand attributes. Forest Ecol. Manage. 128, 109–120.

Jayatissa, L.P., Guero, M.C., Hettiarachchi, S., Koedam, N., 2002. Changes in vegetation cover and socio-economic transitions in a coastal lagoon (Kalametiya, Sri Lanka), as observed by teledetection and ground truthing, can be attributed to an upstream irrigation scheme. Environ. Dev. Sustainability 4, 167–183.

Johnson, E.A., Greene, D.F., 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia – Picea engelmannii* forests. J. Veg. Sci. 2, 523–530.

Juleff, G., 1996. An ancient wind-powered iron smelting technology in Sri Lanka. Nature 379, 60–63.

Kairo, J.G., Dahdouh-Guebas, F., Gwada, P.O., Ochieng, C., Koedam, N., 2002. Regeneration status of mangrove forests in Mida Creek, Kenya: a compromised or secured future? Ambio 31, 562–568.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. Adv. Mar. Biol. 40, 81–251.

Kathiresan, K., 2002. Greeing the blue mud. Rev. Biol. Trop. 50, 869–874.

Keegan, W.F., Portell, R.W., Slapcinsky, J., 2003. Changes in invertebrate taxa at two pre-Columbian sites in southwestern Jamaica, AD 800–1500. J. Archaeol. Sci. 30, 1607–1617.

Kelley, J.T., Barber, D.C., Belknap, D.F., FitzGerald, D.M., van Heteren, S., Dickson, S.M., 2005. Sand budgets at geological, historical and contemporary time scales for a developed beach system, Saco Bay, Maine, USA. Mar. Geol. 117–142.

Kendrick, G.W., Morse, K., 1990. Evidence of recent mangrove decline from an archaeological site in Western Australia (Australia). Austr. J. Ecol. 15, 349–354.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Kovacs, J.M., 2000. Perceptions of environmental change in a tropical coastal wetland. Land Degr. Dev. 11, 209–220.

Kovacs, J.M., Malczewski, J., Flores-Verdugo, F., 2004. Examining local ecological knowledge of hurricane impacts in a mangrove forest using an analytical hierarchy process (AHP) approach. J Coast. Res. 20, 792–800.

Kovacs, J.M., Wang, J., Flores-Verdugo, F., 2005. Mapping mangrove leaf area index at the species level using IKONOS and LAI-2000 sensors for the Agua Brava Lagoon, Mexican Pacific. Estuar. Coast. Shelf Sci. 62, 377–384.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Kumaran, K.P.N., Shindikar, M., Limaye, R.B., 2004a. Fossil record of marine manglicolous fungi from Malvan (Konkan) west coast of India. Indian J. Mar. Sci. 33, 257–261.

Kumaran, K.P.N., Shindikar, M., Limaye, R.B., 2004b. Mangrove associated lignite beds of Malvan, Konkan: Evidence for higher sea-level during the Late Tertiary (Neogene) along the west coast of India. Curr. Sci. 86, 335–340.

Lape, P.V., 2002. Historic maps and archaeology as a means of understanding late precolonial settlement in the Banda Islands, Indonesia. Asian Perspect. 41, 43–70.

Leenders, J.K., Visser, S.M., Stroosnijder, L., 2005. Farmers' perceptions of the role of scattered vegetation in wind erosion control on arable land in Burkina Faso. Land Degr. Dev. 16, 327–337.

Lepofsky, D., Moss, M.L., Lyons, N., 2001. The unrealized potential of paleoethnobotany in the archaeology of northwestern North America: perspectives from Cape Addington, Alaska. Arctic Anthropol. 38, 48–59.

Lewis III, R.R., 1982. Mangrove forests. In: Lewis, III, R.R. (Ed.), Creation and Restoration of Coastal Plant Communities. CRC Press, Boca Raton, pp. 154–171.

Lewis III, R.R., Hodgson, A.B., Mauseth, G.S., 2005. Project facilitates the natural reseeding of mangrove forests (Florida). Ecol. Restor. 23, 276–277.

Lezine, A.M., 1996. The West African mangrove: An indicator of sea-level fluctuations and regional climate changes during the last deglaciation. Bull. Soc. Géol. France 167, 743–752.

Lezine, A.M., Saliege, J.F., Mathieu, R., Tagliatela, T.L., Mery, S., Charpentier, V., Cleuziou, S., 2002. Mangroves of Oman during the late Holocene: climatic implications and impact on human settlements. Veg. History Archaeobot. 11 (3), 221–232.

Lin, S.M., Chen, C.A., Lue, K.Y., 2002. Molecular phylogeny and biogeography of the grass lizards genus *Takydromus* (Reptilia: Lacertidae) of East Asia. Mol. Phylogenet. Evol. 22, 276–288.

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.

MacFarlane, G.R., Pulkownik, A., Burchett, M.D., 2003. Accumulation and distribution of heavy metals in the grey mangrove, *Avicennia marina* (Forsk.) Vierh.: biological indicator potential. Environ. Pollut. 123, 139–151.

Manson, F.J., Loneragan, N.R., McLeod, I.M., Kenyon, R.A., 2001. Assessing techniques for estimating the extent of mangroves: topographic maps, aerial photographs and Landsat TM images. Mar. Freshwater Res. 52, 787–792.

Marguillier, S., van der Velde, G., Dehairs, F., Hemminga, M.A., Rajagopal, S., 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by δ^{13}C and δ^{15}N. Mar. Ecol. Prog. Ser. 151, 115–121.

Mastaller, M., 1997. Mangroves, the Forgotten Forest Between Land and Sea. Tropical Press Sdn. Bhd., Kuala Lumpur.

Menezes, M., Berger, U., Worbes, M., 2003. Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, North Brazil. Wetlands Ecol. Manage. 11, 233–242.

Meynecke, J.-O., 2005. Change under climate change—a strategy to strengthen Australian ecosystems. In: Burk, A.R. (Ed.), Trends in Biodiversity Research. Nova Science Publishers, Hauppauge, pp. 41–80.

Miller, D.L., Mora, C.I., Grissino-Mayer, H.D., Mock, C.J., Uhle, M.E., Sharp, Z., 2006. Tree-ring isotope records of tropical cyclone activity. PNAS 103, 14294–14297.

Moberg, F., Rönnbäck, P., 2003. Ecosystem services of the tropical seascape: interactions, substitutions and restoration. Ocean Coast. Manage. 46, 27–46.

Morton, R.A., 2002. Coastal geoindicators of environmental change in the humid tropics. Environ. Geol. 42 (7), 711–724.

Moseley, R.K., 2006. Historical landscape change in northwestern Yunnan, China—using repeat photography to assess the perceptions and realities of biodiversity loss. Mountain Res. Dev. 26, 214–219.

Mulrennan, M.E., Woodroffe, C.D., 1998. Holocene development of the lower Mary River plains, Northern Territory, Australia. Holocene 8, 565–579.

Mumby, P.J., Green, E.P., Edwards, A.J., Clark, C.D., 1999. The cost-effectiveness of remote sensing for tropical coastal resources assessment and management. J. Environ. Manage. 55, 157–166.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Naylor, R.L., Goldburg, R.J., Mooney, H., Beveridge, M., Clay, J., Folke, C., Kautsky, N., Lubcheno, J., Primavera, J., Williams, M., 2000a. Nature's subsidies to shrimp and salmon farming. Science 282, 883–884.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke, C., Lubchenco, J., Moony, H., Troell, M., 2000b. Effect of aquaculture on world fish supplies. Nature 405, 1017–1024.

Palmer, J., Finlay, V., 2003. Faith in Conservation: New Approaches to Religions and the Environment. The International Bank for Reconstruction and Development/The World Bank, Washington, DC.

Parr, T.W., Sier, A.R.J., Battarbee, R.W., Mackay, A., Burgess, J., 2003. Detecting environmental change: science and society—perspectives on long-term research and monitoring in the 21st century. Sci. Total Environ. 310, 1–8.

Piperno, D.R., 1998. Paleoethnobotany in the Neotropics from microfossils: new insights into ancient plant use and agricultural origins in the tropical forest. J. World Prehistory 12, 393–449.

Plaziat, J., Augustinus, P.G.E.F., 2004. Evolution of progradation/erosion along the French Guiana mangrove coast: a comparison of mapped shorelines since the 18th century with Holocene data. Mar. Geol. 208, 127–143.

Primavera, J.H., 2005. Mangroves, fishponds, and the quest for sustainability. Science 310, 57–59.

Ramsey, E.W., Laine, S.C., 1997. Comparison of LANDSAT Thematic Mapper and high resolution photography to identify change in complex coastal wetland. J. Coast. Res. 13, 281–292.

Rist, S., Dahdouh-Guebas, F., 2006. Ethnosciences—a step towards the integration of scientific and traditional forms of knowledge in the management of natural resources for the future. Environ. Dev. Sustainability 8, 467–493.

Roelants, K., Bossuyt, F., 2005. Archaeobatrachian paraphyly and Pangaean diversification of crown-group frogs. Syst. Biol. 54, 111–126.

Rogers, G.F., Malde, H.E., Turner, R.M., 1984. Bibliography of Repeat Photography for Evaluating Landscape Change. University of Utah Press, Salt Lake City.

Rönnbäck, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol. Econ. 29, 235–252.

Scheel-Ybert, R., 2000. Vegetation stability in the Southeastern Brazilian coastal area from 5500 to 1400 ^{14}C yr BP deduced from charcoal analysis. Rev. Palaeobot. Palynol. 110, 111–138.

Semeniuk, V., 1994. Predicting the effect of sea-level rise on mangroves in Northwestern Australia. J. Coast. Res. 10, 1050–1076.

Smith, J., Lamanna, B., Metthew, C., Lacovara, K.J., Dodson, P., Smith, J.R., Poole, J.C., Giegengack, R., Attia, Y., 2001. A giant sauropod dinosaur from an upper cretaceous mangrove deposit in Egypt. Science 292, 1704–1706.

Schmitz, N., Verheyden, A., Beeckman, H., Kairo, J.G., Koedam, N., 2006. Influence of a salinity gradient on the vessel characters of the mangrove species *Rhizophora mucronata* Lam. Ann. Bot. 98, 1321–1330.

Schmitz, N., Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2007a. Successive cambia development in *Avicennia marina* (Forssk.) Vierh. is not climatically driven in the seasonal climate at Gazi Bay, Kenya. Dendrochronologia 25, 87–96.

Schmitz, N., Robert, E.M.R., Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2007b. A patchy growth via successive and simultaneous cambia: key to success of the most widespread mangrove species *Avicennia marina*? Ann. Bot., doi:10.1093/aob/mcm280.

Souza-Filho, P.W.M., El-Robini, M., 2000. Geomorphology of the Brangaça coastal zone, Northeastern Pará State. Revista Brasiliera de Geociências 30, 518–522.

Souza-Filho, P.W.M., Paradella, W.R., 2002. Recognition of the main geobotanical features along the Brangaça mangrove coast (Brazialian Amazon Region) from Landsat TM and RADARSAT-1 data. Wetlands Ecol. Manage. 10, 123–132.

Souza-Filho, P.W.M., Paradella, W.R., 2003. Use of synthetic aperture radar for recognition of coastal geomorphological features, land-use assessment and shoreline changes in Bragança coast, Pará, Northern Brazil. Anais da Academia Brasileira de Ciências 75, 341–356.

Stafford-Deitsch, J., 1996. Mangrove: The Forgotten Habitat. Immel Publishing Limited, London.

Stein, M., Goldstein, S.L., Schramm, A., 2000. Radiocarbon calibration beyond the dendrochronology range. Radiocarbon 42, 415–422.

Stephens, S.L., Skinner, C.N., Gill, S.J., 2003. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. Can. J. Forest Res. 33, 1090–1101.

Stevenson, J., 2004. A late-Holocene record of human impact from the southwest coast of New Caledonia. Holocene 14, 888–898.

Stevenson, N.J., Lewis, R.R., Burbridge, P.R., 1999. Disused shrimp ponds and mangrove rehabilitation. In: Streever, W. (Ed.), An International Perspective on Wetland Restoration. Kluwer Academic Publishers, Dordrecht.

Stokstad, E., 2001. Myriad ways to reconstruct past climate. Science 292, 658–659.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. Ecol. Appl. 9, 1189–1206.

Taylor, M.P., Lewin, J., 1996. River behaviour and Holocene alluviation: The River Severn at Welshpool, mid-Wales, UK. Earth Proc. Landforms 21, 77–91.

Thampanya, U., Vermaat, J.E., Sinsakul, S., Panapitukkul, N., 2006. Coastal erosion and mangrove progradation of Southern Thailand. Estuar. Coast. Shelf Sci. 68, 75–85.

Theophrastus, 1916. Enquiry into Plants and Minor Works on Odours and Weather Signs. Translated by Hort, A. (1916) Harvard University Press, Cambridge, US.

Theophrastus, 1976. De Causis Plantarum. Translated by Einarson, B., Link, G.K.K. (1976) Harvard University Press, Cambridge, US.

Thom, B.G., Wright, L.D., Coleman, J.M., 1975. Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Old River, Western Australia. J. Ecol. 63, 203–232.

Thom, B.G., 1984. Coastal landforms and geomorphic processes. In: Snedaker, S.C., Snedaker, J.G. (Eds.), The Mangrove Ecosystem: Research Methods. UNESCO, Paris, pp. 3–17.

Thompson, L.G., Davis, M.E., Mosley-Thompson, E., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.-N., Mikhalenko, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J., Francou, B., 1998. A 25,000-year tropical climate history from Bolivian ice cores. Science 282, 1858–1864.

Torrescano, N., Islebe, G.A., 2006. Tropical forest and mangrove history from southeastern Mexico: a 5000 yr pollen record and implications for sea level rise. Veg. History Archaeobot. 15, 191–195.

Triest, L., 2008. Molecular ecology and biogeography of mangrove trees towards conceptual insights on gene flow and barriers: A review. Aquat. Bot. 89, 138–154.

Turner, R.E., Lewis III, R.R., 1997. Hydrologic restoration of coastal wetlands. Wetlands Ecol. Manage. 4, 65–72.

UNESCO, 2003.In: Sixth Meeting of the International Advisory Committee of the Memory of the World Programme (Gdansk, Poland, 28–30 August 2003). UNESCO, Paris.

Vanhecke, L., Charlier, G., Verhelst, L., 1981. Landschappen in Vlaanderen, vroeger en nu./Paysages de Flandre, jadis et aujourd'hui. National Botanical Gardens of Belgium, Meise.

Vannucci, M., 1997. Supporting appropriate mangrove management. International News Letter of Coastal Management-Intercoast Network, Special edition 1, pp. 1–3.

Vedel, V., Behling, H., Cohen, M., Lara, R., 2006. Holocene mangrove dynamics and sea-level changes in northern Brazil, inferences from the Taperebal core in northeastern Para State. Veg. History Archaeobot. 15, 115–123.

Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2004a. Growth rings, growth ring formation and age determination in the mangrove *Rhizophora mucronata*. Ann. Bot. 94, 59–66.

Verheyden, A., Helle, G., Schleser, G.H., Dehairs, F., Beeckman, H., Koedam, N., 2004b. Annual cyclicity in high-resolution stable carbon and oxygen isotope ratios in the wood of the mangrove tree *Rhizophora mucronata*. Plant Cell Environ. 27, 1525–1536.

Verheyden, A., Roggeman, M., Bouillon, S., Elskens, M., Beeckman, H., Koedam, N., 2005a. Comparison between δ13C of α-cellulose and bulk wood in the mangrove tree *Rhizophora mucronata*: Implications for dendrochemistry. Chem. Geol. 219, 275–282.

Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H., Koedam, N., 2005b. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. New Phytol. 167, 425–435.

Verschuren, D., Laird, K.R., Cumming, B.F., 2000. Rainfall and drought in equatorial east Africa during the past 1,100 years. Nature 403, 410–414.

Versteegh, G.J.M., Schefuss, E., Dupont, L., Marret, F., Sinninghe Damsté, J.S., Jansen, J.H.F., 2004. Taraxerol and Rhizophora pollen as proxies for tracing past mangrove ecosystems. Geochimica et Cosmochimica Acta 68, 411–422.

Visser, S.M., Sterk, G., Karssenberg, D., 2005. Wind erosion modelling in a Sahelian environment. Environ. Modelling Software 20, 69–84.

Von Rosenberg, C.B.H., 1867. Reis naar de Zuidoostereilanden gedaan in 1865 op last der Regering van Nederlandsch-Indie. Martinus Nijhoff, 's Gravenhage (in Dutch).

Walters, B.B., 2005. Patterns of local wood use and cutting of Philippine mangrove forests. Econ. Bot. 59, 66–76.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Westgate, J.W., 1994. Eocene forest swamp. Res. Exploration 10, 80–91.

Wang, L., Sousa, W.P., Gong, P., Biging, G.S., 2004. Comparison of IKONOS and QuickBird images for mapping mangrove species on the Caribbean coast of Panama. Remote Sensing Environ. 91, 432–440.

Wang, X., van der Kaars, S., Kershaw, P., Bird, M., Jansen, F., 1999. A record of fire, vegetation and climate through the last three glacial cycles from Lombok Ridge core G6-4, eastern Indian Ocean, Indonesia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 147, 241–256.

Ward, W.T., Little, I.P., 2000. Sea-rafted pumice on the Australian east coast: numerical classification and stratigraphy. Austr. J. Earth Sci. 47, 95–109.

Winchester, V., Chaujar, R.K., 2002. Lichenometric dating of slope movements, Nant Ffrancon, North Wales. Geomorphology 47, 61–74.

WinklerPrins, A.M.G.A., Sandor, J.A. (Eds.), 2003. Ethnopedology. Geoderma. Elsevier, Amsterdam.

Witt, B., 2002. Century-scale environmental reconstruction by using stable carbon isotopes: just one method from the big bag of tricks. Austr. J. Bot. 50, 441–454.

Wolanski, E., Gereta, E., 2001. Water quantity and quality as the factors driving the Serengeti ecosystem, Tanzania. In: Harper, D., Boar, R., Everard, M., Hickley, P. (Eds.), Hydrobiologia 458: Science and the Sustainable Management of Shallow Tropical Waters. Kluwer Academic Publishers, Dordrecht, pp. 169–180.

Woodroffe, C.D., 1999. Response of mangrove shorelines to sea-level change. Tropics 8, 159–177.

Yu, K.-F., Zhao, J.-X., Liu, T.-S., Wang, P.-X., Qian, J.-L., Chen, T.-G., 2004. Alpha-cullulose (13C variation in mangrove tree rings correlates well with annual sea level trand between 1982 and 1999. Geophys. Res. Lett. 31, L11203.

Yulianto, E., Sukapti, W.S., Rahardjo, A.T., Noeradi, D., Siregar, D.A., Suparan, P., Hirakawa, K., 2004. Mangrove shoreline responses to Holocene environmental change, Makassar Strait, Indonesia. Rev. Palaeobot. Palynol. 131, 251–268.

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Review

Long-term retrospection on mangrove development using sediment cores and pollen analysis: A review

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Abstract

Mangroves are biogenic systems that accumulate sedimentary sequences, where cores can provide records of mangrove species variation in distribution with past climate change and sea-level change. Fossil evidence used for palaeoecological reconstruction is based on organic remains that preserve identifying features so that they can be identified to generic levels at least. This includes macrofossils such as fruit, flowers, wood or leaves, or microfossils particularly pollen. Anaerobic conditions in mangrove sediment allow the long-term preservation of these fossil records. Fossil pollen from core samples is concentrated for microscopic examination by use of standard chemical treatments, but refinements of these are necessary for the peculiarities of mangrove peat. Pollen diagrams are expressed in concentrations, or more usefully in mangrove environments as proportions relative to others, as this has been shown to demonstrate the depositional environment actually underneath the mangrove forest. Radiocarbon dating of sedimentary sequences is used to date palaeoecological successions shown by fossil sequences, or long-term sedimentation rates. Sediment accretion in the last 50–200 years can been analysed better using Cs^{137} and Pb^{210} analyses. From pollen and macrofossils mostly recovered from stratigraphic cores of sedimentary rock and more recent sediment, the evolution and dispersal of mangroves through geological time has been reconstructed. While reconstruction of actual temperatures in these earlier records is associative to the fossil types present, it is apparent that mangroves have always been tropical species, extending to higher latitudes only during global warm periods. Many sedimentary records show mangroves deeper than the present lower limit of mangrove growth at mean sea-level. These indicate sea-level rising over time, and mangroves keeping pace with rising sea-level. Stratigraphic dating shows accretion rates of 1 mm a^{-1} for low island locations, and up to 1.5 mm a^{-1} in high islands/continental margins. Sedimentary records can also show die-off of mangroves with more rapid sea-level rise and replacement by open water during rising sea-level, landward retreat of mangrove zones, or replacement of mangroves by freshwater forest with sedimentary infill. The causes of mangrove community changes identified in the palaeoecological record can only be inferred by comparison with ecological studies in the modern environment, the link between the two that may be possible through long-term mangrove monitoring being poorly established.

Keywords: Stratigraphy; Pollen analysis; Palaeoecology; Macrofossil; Sedimentation; Palynology

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1. Introduction

Mangroves are an ecosystem dominated by a diverse yet small group of tropical tree species that have by parallel evolution developed special physiological and morphological adaptations to grow in inter-tidal conditions (Lugo and Snedaker, 1974; Chapman, 1976). Hence, while mangroves are by definition a biogenic community primarily of trees and associated fauna (Duke et al., 2007; Cannicci et al., 2008; Nagelkerken et al., 2008), they do, however, have strong sedimentological associations. This is because their dense vegetation favouring sheltered coastal situations tends to promote sedimentation (Furukawa and Wolanski, 1996; Furukawa et al., 1997; Kristensen et al., 2008). As a consequence mangrove development over geological time can be reconstructed from the fragmented sedimentary records of their own deposits. Being a wet environment, anaerobic conditions of mangrove sediment can allow the long-term preservation of these records.

This paper is a review of mangrove development from research using techniques involving coring of sediment and pollen analysis. There are a range of approaches to mangrove retrospection of which this is part (Dahdouh-Guebas and Koedam, 2008), and does not include biomarker and isotopic studies that can also be used for environmental reconstructions. In many ways there are different approaches, philosophies and objectives in stratigraphic research relative to ecological research. It tends to provide a far longer term perspective on mangrove development, and can also provide information on the adaptation or mortality of mangroves with past environmental changes.

2. Background to core based research

Coring sediment to reconstruct past environments is research guided by a number of assumptions that are different to those used in the ecological studies that dominate the mangrove literature. Walther's Law of Uniformitarianism states that ‘‘The various deposits of the same facies areas and similarly the sum of the rocks of different facies areas are formed beside each other in space, though in cross-section we see them lying on top of each other’’ (Middleton, 1973). The guidance that this gives to core based research is that one core is representative of a whole basin, which is why stratigraphic studies rarely use replication (numerous cores) unless they are looking for finer details of basin sedimentary evolution. The principle also guides that sedimentary units get older with depth, though there may be time disconformities corresponding with either periods lost to erosion, or periods of very low deposition.

Because of the increasing compaction and lithification of older sediments, the resolution of time and sequences of events that can be reconstructed from older sediments gets less. Like all land-based sedimentary sequences the length of record tends to become more fragmentary, unlike offshore sediment where a core can find a sequence of sediment deposits representing the whole Pleistocene or more (Shackleton and Opdyke, 1973). This is rarely possible for the changeable and erosive environment of coastal sediments. Deposits tend to get reworked and hence the fossil records are usually fragmented and have to be related from site to site. Deposits which are exposed tend to oxidise and lose their palaeo-records.

Fossil evidence of mangroves is either as macrofossils (fruit, flowers, wood or leaves) or microfossils. Microfossils include organic remains that preserve identifying features that they can be identified to generic levels at least. From coastal environments, these include a range of indicators such as dinoflagellates, foraminifera, diatoms and palynomorphs. The only specific indicators in this group of mangrove environments are mangrove pollen.

The occurrence of mangroves on shorelines means that fruits or pollen can be carried by tides or currents before entering a fossil forming situation. This points out a problem in use of isolated mangrove pollen grains or macrofossils such as disseminules to interpret from a fossil sample that this was a mangrove environment. Mangrove pollen particularly can extend far offshore from mangrove shorelines and end up in low concentrations in marine or coastal sediment.

2.1. Coring

A core is usually taken from a location in the swamp representative of the larger area, the author always places a transect through the centre of the swamp from landward to seaward, and cores systematically along this. This reduces the influence of usually local land based edge effects, and maximises the record of influence of non-local factors such as climate and sea-level. The corer used depends upon the research question, the amount of sample needed for the analysis planned, logistics such as access and sediment depth, and equipment availability. Hand operated piston corers such as Livingstones allow the recovery of an intact core tube able to be later analysed for micro-stratigraphy using techniques such as X-ray, and also allows later choice of levels from which to take pollen or radiocarbon dating samples. However, such piston corers are better suited for lake sediment and can be difficult to penetrate through estuarine sediment, and in roots and other macrovegetation remains cores can be subject to compaction. Mechanised corers such as vibrocorers work in a similar manner, and allow greater depth penetration and retrieval.

Sidewall samplers such as Davis, D section or Hiller corers like hand piston corers can be easily used to depths of 10–15 m. They have an auger action which allows easier penetration through mangrove roots, sand facies and wood. They also ensure no compaction through the sidewall sampling mechanism, so are better for research questions where elevation and depth are critical such as sea-level reconstruction. The disadvantage of these corers is that the sediment is scraped into the chamber so finer details of stratigraphy can be lost, and must then be sub-sampled from the chamber. The intact core is generally not able to be preserved for later description.

For microfossil research, it is best to core at low tide, and sample contamination is further prevented by dismantling and washing the corer each time used, and wiping tools such as spatulas used for sub-sampling. To avoid contamination from raising the corer through upper layers for each core section, the core sampler is washed off before opening the cylinder.

2.2. Radiocarbon dating

Radiocarbon dating can be used to date fossil carbon in cores which has been buried from contact with any decaying process such as oxidation, and can provide dates at best between 400 and 50,000 years old, the limits of radiocarbon dating being 30,000–50,000 years. Samples for radiocarbon dating analysis are removed from the corer, cleaned as above, using a metal spatula and deposited onto unoiled aluminium foil.

Samples are usually pre-treated by first picking for any apparent rootlets, and dried. Then washed in hot 10% HCl, to eliminate carbonates, rinsed, then washed in hot 10% NaOH for 1 h. Samples are then centrifuged with distilled water and the soluble material discarded. The insoluble fraction is retained and acidified using hot 10% HCl, rinsed and dried. The insoluble fraction can then be counted by conventional beta decay techniques. Accelerated Mass Spectrometry (AMS) dating is used where samples are not large, and where the error margin needs to be tighter than that available from conventional techniques. AMS also has the advantage of being able to date small fragments (wood, leaves, etc.).

Radiocarbon dates are corrected for fractionation error using the ^{13}C:^{12}C ratio determined for each sample. Dates are reported in conventional radiocarbon years before present (BP), based on the Libby half-life of 5568 years. They can be calibrated to calendar years by comparison of radiocarbon dates with samples of known age from tree rings (Stuiver et al., 1998), which can be done using Web-based programs such as OxCAL.

2.3. Lead 210 and Cesium 137 dating

Sediment accretion in the last 50–100 years has been analysed from mangroves using ^{137}Cs and ^{210}Pb analyses (Lynch et al., 1989; Ellison, 1989; Cahoon and Lynch, 1997; Gilman et al., under review). This period cannot be dated using ^{14}C due to the fossil fuel emission disruption of the ^{14}C:^{12}C ratio in the atmosphere. The ^{210}Pb input to the sediment from atmospheric deposition is referred to as ‘‘unsupported’’ or ‘‘excess’’ lead activity (Lynch et al., 1989), and ^{210}Pb activity in sediments is derived from the decay of its parent ^{226}Ra, referred to as ‘‘supported’’ ^{210}Pb activity. The half-life of ^{210}Pb is 22.3 year, and the decay of the excess ^{210}Pb is used to determine sediment accretion rates, assuming there is uniform and constant input of lead to the sediment surface, and a constant accretion rate (Lynch et al., 1989). If so, then there will be an exponential decrease in ^{210}Pb activity with depth that can be used to estimate sediment accretion rates (Donnelly and Bertness, 2001).

Cesium-137 (half-life 30.17 years) is an artificial radionuclide distributed across the earth's surface due to fallout from atmospheric nuclear tests and accidental releases from nuclear reactors. Widespread global distribution of ^{137}Cs began with the first atmospheric atomic explosion in Hiroshima in 1945, expanding with atmospheric testing of nuclear weapons during the 1950s and 1960s. 1963 is the year of maximum global cesium fallout and 1954 is the year of first significant ^{137}Cs fallout (DeLaune et al., 1978; Lynch et al., 1989). The thickness of sediment above the sediment horizon with the ^{137}Cs peak can be used to estimate the average sediment accretion rate since the deposition of this horizon in 1963 (Lynch et al., 1989).

Sediment cores for these techniques require wide diameter intact cores that can be cut into volumetric slices. Slicing must be done with clean steel and plastic tools to 2–4 cm intervals, storing in samples in plastic sacks, and kept frozen throughout storage and transport.

2.4. Pollen analysis of mangrove sediments

A pollen grain is the male gametophyte of a flowering plant, while a spore is the gametophyte producing cell of a lower plant. According to dispersal strategy, the quantity produced varies between species. Wind pollinated species such as *Rhizophora* produce large amounts, while insect pollinated species such as *Hibiscus* (a mangrove associate) produce much less pollen and their pollen are much less easily dispersed so that insect pollinated taxa rarely have pollen that appears in the fossil record. Both pollen and spores have an outer covering that is resistant to decay in anaerobic conditions, which by features of shape, size, aperture type and ornamentation can be identified to species level in many plants. Identification of pollen is generally to genus level, and sometimes to species level. Pollen descriptions can either be obtained from the published literature, or for new sites for pollen research a key of pollen can be developed from a reference collection.

A reference collection is developed by collecting anthers from the mature flower of species one wishes to describe, then treating these to a reduced version of the pollen concentration procedure below. The only stages necessary in this case should be hydrolysis of humic compounds, acetolysis and dehydration.

Pollen from reference samples is processed, and surface and core samples concentrated by use of standard chemical treatments as described by Erdtman (1969) and Faegri and Iversen (1975), but refinements of these are necessary for the peculiarities of mangrove peat (Chappell and Grindrod, 1985; Grindrod, 1988). As mangrove vegetative matter is particularly resistant, an oxidation stage is best included, using bleach (NaClO), necessitating that pollen is later stained to render it visible. Silicone oil or cinnamon oil is better used to mount mangrove pollen so that the microscopist can turn the pollen over for identification, an approach needed to distinguish pollen types within the Rhizophoraceae.

Pollen concentration can also provide additional information on the frequency of the occurrence of mangrove taxa, and provide quantitative comparison of pollen influx. Absolute concentration of pollen is where quantities present can be described in grains cm^{-3}. This can be determined by addition of a known number of exotic pollen to a measured volume of the sediment prior to commencing pollen concentration (Benninghoff, 1962). Grindrod (1985) determined absolute pollen concentrations by purely volumetric sampling methods, and encountered problems with samples containing coarse sediments, and with losses from the sample during laboratory preparation. Use of exotic pollen grains avoids these problems as the exotic pollen are lost during the process at presumably an equivalent rate to the fossil pollen, so remain proportionally representative (Benninghoff, 1962). Concentration can then be determined by the following equation:

$$\text{concentration(grains/cm}^3\text{)} = \frac{\text{total no. exotics added}}{\text{no. of exotics counted}} \times \frac{\text{no. of fossil pollen counted}}{\text{volume of subsample}}$$

The pollen sample preparation technique involves removal of other material from the sediment leaving the pollen along with other similar resistant materials such as charcoal, sponge spicules, cysts and usually a fascinating array of other microscopic items. The pollen concentration procedure commonly used by the author is described below, and is best carried out in a fume cupboard.

At all stages in the sample handling and preparation procedure, it is necessary to apply strict quarantine of samples from each other such as washing and wiping the volumetric sampling device between samples, and keeping stirring sticks for each sample apart to prevent cross contamination.

Pollen analysis is usually conducted on 10 cm interval sub-samples from cores, which since collection should be stored in a cool place to prevent drying out. From a core or surface sample a sub-sample of 1 cm^3 is placed in a 15 ml polypropylene test tube. Add usually two exotic pollen tablets, e.g. *Lycopodium*, though the amount depends on the pollen concentration present and can be determined early in the laboratory proceedings by some microscope reconnaissance. It is best to have the exotic pollen roughly equivalent in concentration to the fossil pollen.

Calcium carbonate sediment is removed by adding 10% HCl, and stirring with a wooden applicator stick while placed in a warm water bath. This stage may not be necessary for cores from sites with little carbonate sediment, but from carbonate settings such as limestone islands effervescence can be violent, and this phase may have to be repeated as many as five times to eliminate any calcareous lagoon sediment.

Change of liquid between stages is achieved by centrifuging at 3500 rpm for 5 min, and decanting the supernatant into a safe chemical disposal area. The number of samples that can be run at once is usually determined by the capacity of the centrifuge. Distilled water is then used to wash samples after the HCl stage.

For removal of humic compounds, 10% NaOH or 10% KOH is added, and test tubes placed in a hot water bath for 15 min, stirring and adding distilled water to prevent increased concentration by evaporation. Then washing is repeated until the supernatant runs clean, as many as eight times for mangrove peat. Difficulty in cleaning at this stage can be an indication that the sample had at some stage been oxidized. This stage may not be necessary for sediment that is mostly inorganic.

Sediment then dispersed by NaOH, the sample is passed through a 150 μm sieve to remove large organic fragments. The sample is then reconcentrated.

The hydrofluoric acid (HF) treatment is used to remove silicates, and for this reason a polypropylene test tube was used not glass. HF is quite dangerous and appropriate care should be taken. Samples are boiled in HF in a hot water bath for an hour, or can be left overnight at room temperature. In some situations, the HF treatment to remove silicates is not used (Ellison, 1989, 1993), as it may be desirable to keep sedimentary records of ash falls and deposition of siliceous sponge spicules for examination. Where the sediment source of the site is siliceous it is necessary (Ellison, 2005), but on low carbonate island sites, for example, it can be omitted. As before, after decantation of HF the sample must be washed.

Acetylosis is then necessary to render the pollen wall ornamentation more visible. Samples are first washed in glacial acetic acid mainly to eliminate water with which acetic anhydride violently reacts, then a 9:1 mix of acetic anhydride and concentrated sulphuric acid added. Test tubes are placed in a hot water bath for up to but not exceeding 10 min, then washed again with glacial acetic acid, then distilled water.

For oxidation, 3% bleach is added, and diluted and removed according to the speed of the reaction. The sample is then washed. Towards the end of the procedure, for dehydration, 50% ethanol is added, then two drops of safranin stain (optional), then 75% followed by 95% ethanol. Then tertiary butyl alcohol is added, the test tubes centrifuged and decanted, and transferred to labelled glass storage vial in this alcohol. Silicone oil is added, and vials left at 47 °C to evaporate off the alcohol to leave the pollen preserved in silicon oil. From this slides can be made.

Pollen and spores are identified by comparison with a reference collection, and counted from slides by systematic transects, with a count of preferably 300 pollen per slide, because some taxa, i.e. *Avicennia* occur infrequently. Pollen and spore results are expressed in percentages, or absolute concentration data. In some sediments, results show that the pollen concentration is too low for reliable analysis, for example, the lagoon sediments in Ellison (1989) and mangrove cores of Vishnu-Mittre and Guzder, 1973).

Pollen and spores, and exotic *Lycopodium* spores are identified and counted on exclusive transects on each slide. Counting should be continued until a total of 200 fossil pollen and spores is exceeded. Other microfossils present such as charcoal, mycoflora and in case no HF has been applied sponge spicules and diatoms can be described and counted. While most mangrove species can be distinguished from their pollen, Muller and Caratini (1977) described groups within *Rhizophora* species that practically cannot be distinguished with certainty on the basis of their pollen characters. For example, in triporate *Rhizophora* pollen, *R. stylosa* and *R. mucronata* both have psilate-reticulate-perforate ornamentation, and *R. apiculata*, *R. lamarkii* and *R. mangle* all have reticulate-rugulate ornamentation. It is possible to distinguish between these groups, but not within them. Similarly, the pollen of *Bruguiera* and *Ceriops* are indistinguishable under the light microscope (Grindrod, 1988).

Results are plotted into pollen diagrams using software such as TILIA and TILIAGRAPH (Grimm, 1988). The pollen diagrams include summaries of the total data recorded, the relative representation of each taxon recorded in samples down each core, and the concentration of selected taxa. Pollen taxa can be grouped into ecological categories including mangroves, non-mangrove trees and shrubs, herbs, aquatics and unknowns. Fern spores and other palynomorphs (fungal spores, organic foraminifera-linings, dynoflagellate cysts and chlorophylleae) are best excluded from the pollen sum and shown as percentages of the total sum (total sum = pollen + spore sum). Charcoal particles are microscopic charcoal derived from burnt vegetation that are identified as opaque, angular particles >10 μm in size and can also be shown, indicative of fires in the catchment.

2.5. Pollen diagram interpretation

Most pollen analysis research has examined sequential fossil pollen deposits for reconstruction of past vegetation patterns from a lake or bog core, with climatic change implications (Kershaw, 1976; Flenley, 1979). There could be reason to expect that open-system intertidal and nearshore sediments would not offer the sensitive record of closed systems such as lakes and bogs where pollen analysis of past vegetations is traditionally performed. Sediment mixing from turbulence and bioturbation could provide the means for extensive pollen redistribution (Chappell and Grindrod, 1985).

However, early studies of pollen in surface samples within the mangrove ecosystem showed that there is a high *Rhizophora* proportion in and immediately adjacent to the *Rhizophora* zone (Muller, 1959; Cohen and Spackman, 1977), and this was utilized as a sea-level indicator. Wijmstra (1969) used modern surface samples from mangroves to interpret fluctuations of sea-level from the Cretaceous to the Plio-Pleistocene in Surinam, identifying a 90% proportion of *Rhizophora* as a *Rhizophora* stand, and a 30% proportion as immediately adjacent to a *Rhizophora* stand such as a seaward mud flat. Bartlett and Barghoorn (1973) used similar conditions to interpret the Holocene transgression from Panama, that between 45% and 95% of *Rhizophora* plus *Avicennia* represents a mangrove swamp of these species, and 45–10% *Rhizophora* pollen, declining to less than 10% represents sediments immediately landward of mangroves. Extensive work from 20 years ago in tropical Australia fully established the value of pollen analysis of mangrove sediments to environmental reconstruction. High proportions of mangrove pollen were found to indicate a mangrove environment, declining to 50% or less immediately adjacent (Grindrod and Rhodes, 1984; Grindrod, 1985, 1988; Chappell and Grindrod, 1985; Woodroffe et al., 1985; Behling et al., 2001).

This finding has led to the use of percentage pollen diagrams to interpret mangrove environments as opposed to pollen concentration diagrams that are commonly used in studies that reconstruct vegetation change as a result of climate change over time.

3. Core records of mangrove evolution and response to climate change

The evolution and dispersal of mangroves has been reconstructed from a range of studies of fossil deposits, and this subject has been reviewed substantially already (Plaziat et al., 2001). Saenger (1998) and Ellison et al. (1999) provide useful tabular summaries of these sources. Mangroves first appeared in the Late Cretaceous (from 69 million years ago) within the Tethys Sea at mainly equatorial latitudes, and dispersed along coastlines. The earliest mangrove to appear was *Nypa*, identified from pollen and macrofossils, which is substantially different from the other mangrove species being a palm without a trunk. It also favours low salinity landward edge locations in the mangrove environment.

The mangrove adaptation among angiosperms started during the late Paleocene in the S.E. Asia/S.W. Pacific region, as indicated by the high diversity of mangrove taxa there today (Chapman, 1975, 1976; Hadac, 1976; Triest, 2008). This is shown by pollen records of *Rhizophora*, an excellent source of evidence as the genus produces vast quantities of pollen, being anemophilous, and these are of a type that cannot be confused with pollen of other species. In Borneo, *Rhizophora* pollen is absent from Cretaceous and Paleocene sediments, perhaps first appearing in Eocene sediments, and is certainly present in the Oligocene (Muller, 1964). Other mangrove species evolved, however, at different geological periods, dispersed at different rates from different locations and developed different adaptive strategies (Duke, 2002). The latitudinal distribution of mangroves increased over this period of evolution, up to 50°N and S (Plaziat et al., 2001).

In America, palynomorphs of *Nypa* and *Pelliceria* occur from the early Eocene (Graham, 1995) and the middle Eocene (Westgate and Gee, 1990) and macrofossils of *Rhizophora* are recorded from the Middle Eocene of Georgia (Berry, 1914). From the 300 m deep Alliance Well in Surinam, S. America, strong presence of *Rhizophora* pollen is shown from the Upper Eocene at 180 m depth and above (Wijmstra, 1969: 130). Rull (1998) found mangrove pollen of *Pelliciera* and *Nypa* in Paleogene sediments of Venezuela. In the Caribbean, *Rhizophora* pollen is certainly absent in pre-Eocene sediments, appearing in the upper Eocene, and reaching high percentages in the Miocene (Germeraad et al., 1968). *Rhizophora* pollen is present in Oligocene to Lower Miocene sediments from Brazil (De Boer et al., 1965), the Oligocene of Puerto Rico (Graham and Jarzen, 1969) and from the Oligo-Miocene in Mexico (Langenheim et al., 1967). *Avicennia* is first reported from the late Miocene (Graham, 1995).

In Australia, pollen evidence of mangroves is found in Middle to Late Eocene shales laid down during a global sea-level highstand that flooded much of the Australia continent. In an event marking the start of the Eocene, the Paleocene-Eocene Thermal Maximum upset oceanic and atmospheric circulation and led to the extinction of numerous deep-sea benthic foraminifera, and a major turnover in land mammals (Kennett and Stott, 1991). These parts of Australia at that period were around 50°S (Plaziat et al., 2001). Temperatures fell towards the end of the Eocene and continued general decline through the Miocene towards the Pliocene.

Reconstructing the climatic conditions of these early mangrove floras is, however, very difficult by comparison to the time resolution and precision possible using isotopic analysis of Pleistocene foraminiferal cores (Shackleton and

Opdyke, 1973). Dating of older rocks generally uses biostratigraphy, using the succession of fossil species of animals and plants that are found in successive strata of rock, and association with geological type-sites. The time periods covered by small sequences are also very long. Hence, the climatic conditions inferred as those of association, tending to be qualitative not quantitative.

Around 18 million years ago, the western end of the Tethys Sea became isolated with the enclosure of the Mediterranean by the collision of Africa and southern Asia (Saenger, 1998). At that time the pantropical mangrove flora became disjunct and subsequently developed independently, leading to the different species of the S.E. Asian and American centres of mangrove biodiversity of the mangrove genera common between both. Finally, around 3 million years ago the Panama Gap closed with the collision of North and South America, to disjunct the mangroves on either side of the American landmasses.

The pollen record does not show clear trends of mangrove migration with climate change, more distributions have changed over time more due to biogeographic factors and habitat availability. This is exemplified by records in the Pacific Islands, where mangroves of the New Guinea centre of biodiversity today reach a eastern limit at American Samoa (Ellison, 1995). Leopold (1969) showed distributions of mangroves in the west and south Pacific to be far more extensive in the past than at present, recording *Rhizophora*, *Sonneratia*, *Avicennia* and *Scyiphora* pollen from the Miocene of Enewetok Atoll, Marshall Islands. All of these species have more restricted distributions today. Leopold suggested that, at times, post-Miocene Enewetok was completely submerged, necessitating later recolonization by plants, which may explain the local extinction of *Rhizophora*. In Miocene dark peat sediments on Viti Levu, Fiji, Ladd (1965) found pollen of *Sonneratia*, which today extends only east as far as Vanuatu.

Further evidence of the now reduced ranges of mangroves as a result of habitat loss not climate change comes from the Cook Islands, where mangroves are today absent. On Mangaia, Ellison (1994) cored lakes to find *Rhizophora* pollen (probably *R. stylosa*) for periods during the Holocene. This reached a high concentration of 2691 grains cm^{-3} and occurred around 7250, 5000 and 2000 years BP, when man arrived 2500 BP. *Rhizophora* was not previously believed to be indigenous east of Samoa (Ellison, 1991), and seems to have colonised the inner swamps of Mangaia through conduit caves. The loss of *Rhizophora* from Mangaia as shown in the pollen diagrams could have been caused by decreasing salinity of the inner swamps with sea-level fall, and closure of the conduit caves by sedimentation.

The paleoecological record therefore gives evidence that habitat suitability for mangroves is controlled by sea-level elevation relative to land surfaces, and rates of sea-level change. However, in Holocene studies small range extensions during warmer conditions have been shown. Mildenhall and Brown (1987) found pollen of *Avicennia marina* at 9800 years BP further south on the New Zealand coast than its present ranges, and Mildenhall (1994) found another site 9 km further south of this, inferring an Early Holocene climatic warm period of perhaps 1 °C higher. However, the pollen percentages were very low at both sites.

4. Core records of mangrove evolution and response to sea-level change

Given that mangroves generally grow between mean sea-level and mean high water, their sedimentary records have been used as both directional and precise sea-level indicators. Other indicators such as coral can grow at a variety of depths, while wave cut notches can give an accurate height but provide little to date (Ellison, 1989). Such research has recently gained significance in providing reconstruction of how mangroves responded to past sea-level changes, with growing indication that global eustatic sea-level are no longer stable (Gilman et al., 2008). Comparing present trends in species and communities with palaeoecological records of past extents provides excellent information on how they may respond to climate change (Hansen et al., 2001; Hansen and Biringer, 2003).

Mangrove development has been examined in detail in the Florida Everglades mangrove complex, and shown to be controlled by Late Holocene rates of sea-level rise (Scholl and Stuiver, 1967; Scholl et al., 1969). Pollen analysis of cores by Cohen and Spackman (1977) showed a transgressive sequence from basal freshwater peats, through mangrove peats, to marine carbonate mud. Significant shoreline retreat was demonstrated over the last 5000 years, with peats under calcareous mud extending at least 2.4 km offshore. At this margin, pollen analysis of peat from 3 to 4 m below sea-level showed freshwater peat in the lower 50 cm and mangrove peat in the upper 50 cm. Parkinson (1989) traced peats of <1 m thickness up to 4 km offshore of the 10,000 Islands mangrove area, at 4–5 m below present sea-level. This transgressive sequence occurred before 3500 ^{14}C years BP (before present) during more rapid sea-level rise. Subsequently, mangrove peat accumulation was able to keep pace with more slowly rising sea-level, allowing stabilization of the coastline and development of deep peats.

The Cayman Islands similarly experienced a slowly rising sea-level to present levels during the Holocene. Offshore coring transects found a mangrove peat under the present seagrass beds of the whole of the Little Sound lagoon, and the eastern portion of the North Sound. The margins are shown in Fig. 1, showing that the area of mangroves that has died off is about 19.8 km^2. The upper surface of this peat unit is at similar depths, mostly between 3 and 4 m below present MSL. The thickness of the peat was around 3 m (down to 6 m below present sea-level). The radiocarbon dates from peat immediately below the calcareous sand in four spatially separated cores show good correlation, all within the range of 3230 and 4080 radiocarbon years before present. These dates could be older than the die-off event for two reasons: the peat dated would have formed under a healthy forest before the disruption, and erosion of the peat surface probably occurred during the dieback. Pollen analysis of a core taken at the present mangrove seaward margin indicates that during existence of the fossil mangrove area, this was the landward mangrove zone. In upper

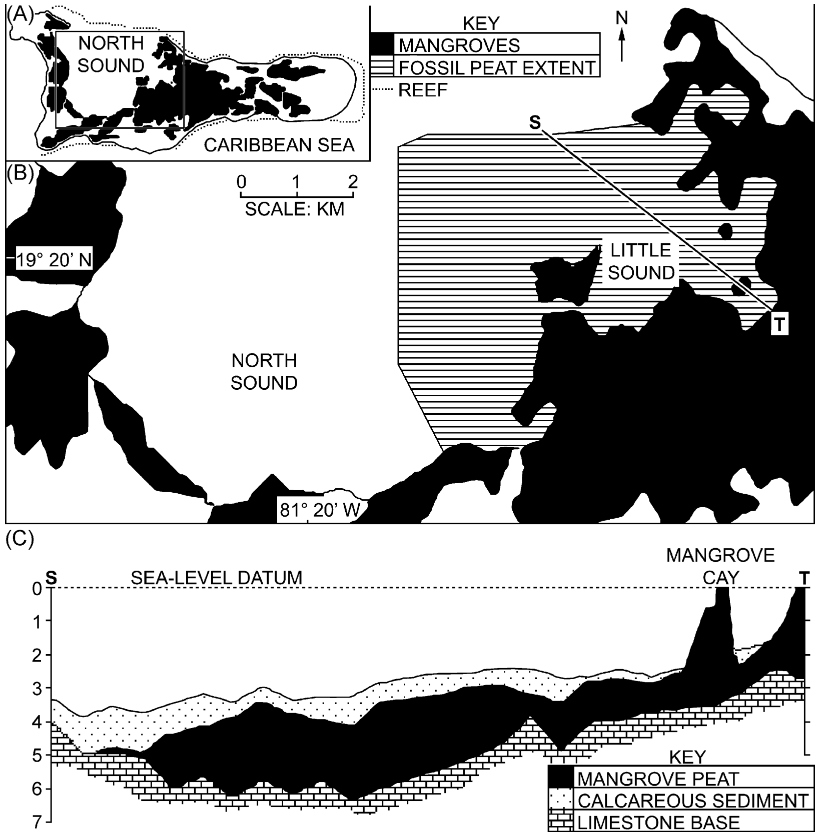

Fig. 1. (A) Mangrove distributions on Grand Cayman, Cayman Islands. (B) Former and current mangrove extents in the North Sound, Grand Cayman. (C) Holocene stratigraphy of the transect shown in B.

sections of the core, percentages of *Rhizophora* pollen increased indicating retreat of mangrove zones landward with sea-level rise.

There are further numerous examples in the mangrove stratigraphy literature of Holocene mangrove sediment occurring to deeper than the present lower limit of mangrove growth at mean sea-level (Laeyendecker- Roosenburg, 1966; Roeleveld, 1969; Bloom, 1970; Bartlett and Barghoorn, 1973; Haseldonckx, 1977; Ellison, 1989; Berdin et al., 2003; Behling et al., 2004; Wooller et al., 2004; Cohen et al., 2005; Ellison, 2005). These generally indicate that sea-level have risen over the mid- to late-Holocene and mangroves have kept pace with rising sea-level. With present projections of increased eustatic sea-level rise, records of mangroves that keep up then die back with increased sea-level rise rates are of concern, as did this now submerged North Sound mangrove forest around 4000 years BP in Cayman.

The deep Holocene stratigraphy below the coastal mangroves of the Federated States of Micronesia was first described by Bloom (1970). Fujimoto (1997) coring mangrove sediment of Kosrae found that most of the mangrove forests have been developed during the last 2000 years by accumulating mangrove peat with the gradual sea-level rise of 1–2 mm a^{-1}. During the period of rapid sea-level rise of about 10 mm a^{-1} between 4100 and 3700 years BP, the mangrove forests ceased peat accumulation and retreated landward. These evidences suggest that the critical rate of mangrove peat accretion with sea-level rise is between 2 and 10 mm a^{-1}.

In Tonga, the largest area of mangroves occurs in the western Fanga'uta Lagoon on Tongatapu (Ellison, 1989). The stratigraphic diagram in Fig. 2 shows mangrove peat occurring between about 2.5 and 1.5 m below present sea-level, indicating a large mangrove swamp that persisted between 7000 and 5500 years BP during sea-level rise reconstructed to be at a rate of 1.2 mm a^{-1}. Then sea-level rose again to a mid-Holocene highstand about 1 m above present sea-level around 5500 years BP, and this mangrove area died back to become a lagoon. The mangrove swamp later re-established over the whole site following sea-level fall in the later Holocene.

In Bermuda at the northern limit of mangroves in America, two pollen diagrams from the largest mangrove area showed vegetation changes over the last 5000 years (Ellison, 1996). From 5000 to 2100 years ago, the swamp was a marsh wetland, and pollen evidence is also shown of the dryland endemic forest before colonization of Bermuda. Establishment of mangroves only occurred in the last 3000 years, when sea-level rise slowed from 26 to 7 cm/100 years. This confers with the record from Florida, where expansive mangroves did not establish until after 3500 years BP (Scholl, 1964), and with records from the eastern Pacific showing that mangroves expand and contract their ranges with habitat availability (Ellison, 1994). The Hungry Bay mangrove swamp then existed for the last 2000 years during a period of sea-level stability, but during the last century lost 26% of its area due to retreat of its seaward edge (Fig. 3).

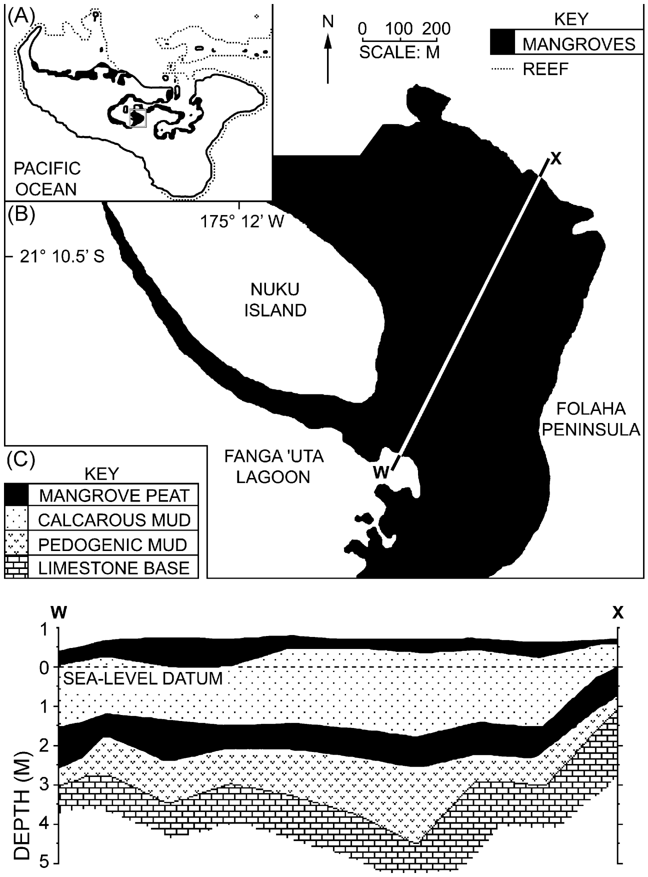

Fig. 2. (A) Mangrove distributions on Tongatapu, Tonga. (B) Mangrove swamp at Folaha, Tongatapu. (C) Holocene stratigraphy of the transect shown in B (adapted from Ellison, 1989).

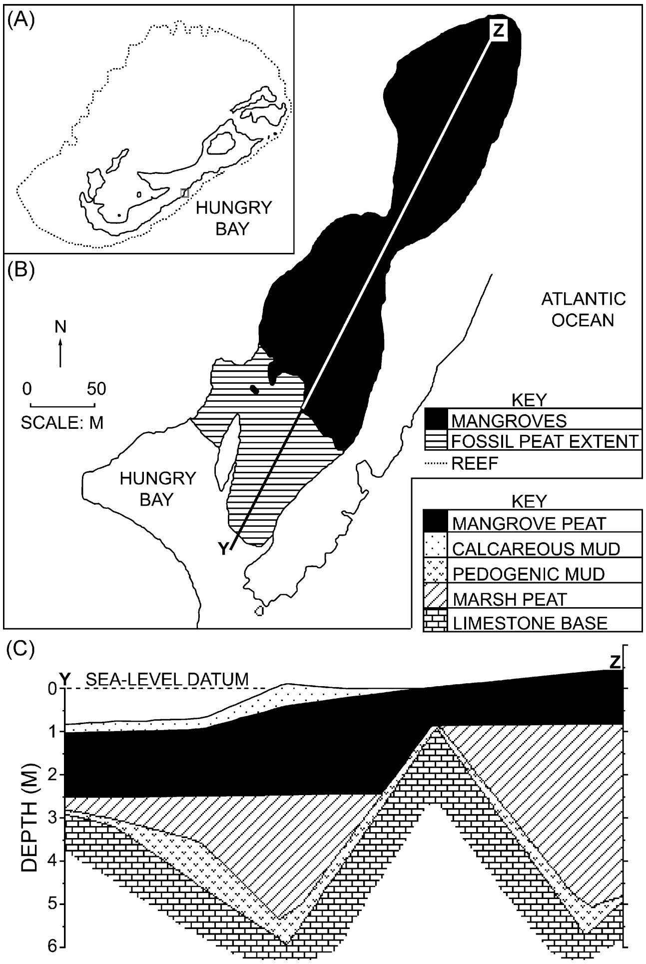

Fig. 3. (A) Location of the Hungry bay mangrove swamp, Bermuda. (B) Former and current mangrove extents at Hungry Bay. (C) Holocene stratigraphy of the transect shown in B (adapted from Ellison, 1993).

Erosion of mangrove sediment during rising sea-level does cause loss of record such that interpretation of continuity of events is more difficult. In Grand Cayman, at the lagoon edge of the coring transect where mangrove peat occurs beneath open water (Fig. 1), and peat cliffs can occur at the edge of the present mangroves. This could be caused by current and wave erosion at the mangrove margin. Today in the lagoon a depositional environment exists, shown by calcareous sediment derived from seagrass beds developed above the fossil mangrove peat (Fig. 1).

This Bermuda site demonstrates that mangrove sediment is subject to erosion by rising sea-level, with removal of mangrove substrate (above MSL) and with some deposition subtidally offshore of the mangroves (Ellison, 1993). Similar erosion patterns to Bermuda, with reversed succession as elevation declines, have been described by Semeniuk (1980) in N.W. Australia. The effect of sheet erosion on mangrove zonation is migration of pioneer/seaward mangroves into more landward zones. The result of this to the stratigraphic record is a discontinuity in the sequence of deposits, removing a section of older material such that it is lost from the core record.

Another example of this occurrence is Northern Territory of Australia, where Woodroffe and Mulrennan (1993) have documented dramatic recent changes to the Lower Mary River floodplain, with saltwater intrusion and upstream expansion of the tidal creek network. This has resulted in the death of freshwater wetland communities with loss of 60 km^2 of *Melaleuca* forest and upstream invasion of mangroves. There are a number of possible reasons for these events, including relative sea-level rise (Woodroffe, 1995). Similar, though less spectacular, extension of creeks has occurred on other river systems such as the Alligator rivers (Woodroffe, 1995). Loss of freshwater wetlands with saline intrusion is documented in the Florida Keys (Ross et al., 1994), where longer tide records have enabled researchers to attribute the cause to relative sea-level rise. Erosion of surface sediments with intrusion occurs to varying degrees, but obviously along creek banks and where sediment is destabilised by covering vegetation mortality.

Gradual retreat of mangrove zones with slowly rising sea-level has also been demonstrated from the extensive coastal swamps of southern New Guinea (West Papua) (Ellison, 2005). Fig. 4 is a long pollen diagram covering over 9000 years from the Tipoeka Estuary showing a *Bruguiera* zone present at the core site for most of the Holocene, replaced around 3000 years ago by a *Rhizophora* zone. This sequence of events was replicated at 4 other core sites throughout this and the adjacent Ajkwa Estuary. The elevation of this transitional zone in the

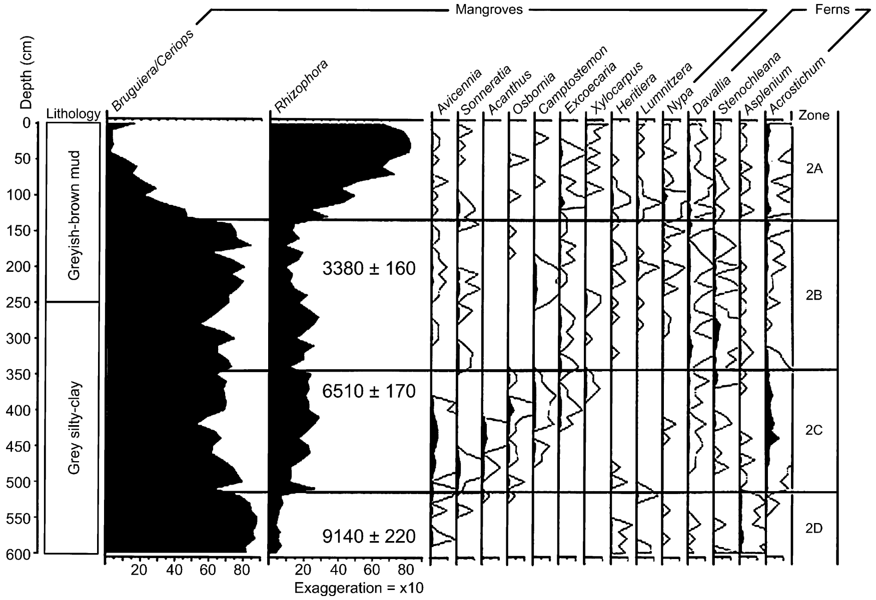

Fig. 4. Holocene mangrove pollen diagram from the Tipoeka Estuary, southern New Guinea (adapted from Ellison, 2005).

present day mangrove swamp was surveyed to be 1.6 m above MSL, and this was used as a finite sea-level indicator to interpret rates of sea-level rise from these cores. Landward *Bruguiera* being replaced by seaward *Rhizophora* indicates landward retreat of the mangroves with slowly rising sea-level, at a rate of sea-level rise determined to be only 0.67 mm a^{-1}.

These palaeoenvironmental records of mangroves from a number of locations with different Holocene sea-level curves all shown sensitivity to sea-level rise, including dieback and massive mortality events. Sediment supply determines mangrove ability to keep up with sea-level rise. Mangroves of low relief islands in carbonate settings that lack rivers are shown to be the most sensitive to sea-level rise, owing to their sediment-deficit environments. However, as demonstrated from southern New Guinea, continental mangroves (such as mainland Australia) also demonstrate migration and relocation inland. In summary, radiocarbon dating of stratigraphy determined a sediment accretion rate of 1 mm a^{-1} for the low island locations, and up to 1.5 mm a^{-1} in two estuaries of southern New Guinea.

This rate is of significance because within the intertidal habitat of mangroves, species have different preferences for elevation, salinity and frequency of inundation, resulting in species zones. Elevation of the ground surface under mangroves can be raised, by accumulation of vegetative detritus or inorganic matter brought in by tides or rivers. If the sedimentation rate keeps pace with rising sea-level, then the salinity and frequency of inundation preferences of mangrove species zones will remain largely unaffected. If the rate of sea-level rise exceeds the rate of sedimentation, then mangrove species zones will migrate inland to their preferred elevation, and seaward margins will die back. The accumulation of sediment under mangroves will help to compensate for rising sea-levels.

5. Conclusion

Core based research allows a longer term perspective of mangrove development at suitable sedimentary sites, and can show migration and mortality with environmental changes of the past. It is part of a range of retrospection approaches available (Dahdouh-Guebas and Koedam, 2008). The use of pollen analysis can give detail on the species present and the longer term changeover between these such as landward species zones giving to seaward zones over time. The elevations of these in the modern environment can also be used to interpret details of former sea-level and sedimentation rates from cores.

Mangroves are extremely important for local inhabitants (Hamilton and Snedaker, 1984; Walters et al., 2008), and core-based research can provide insight into man–ecosystem relationships. This can include changes in the mangrove community structure, as well as changes in sedimentation rates reflecting catchment disturbance (Ellison, 1994).

While core records have the benefit of showing site evolution over centuries and millennia, the time resolution of the record is, however, limited and blurred into overall long-term consequences. Hence, while the palaeoenvironmental record of mangroves shows their sensitivity to sea-level rise, including dieback and massive mortality, the causes of this mortality is not apparent from this source. Causes such as inundation stress, change in salinity, or other factors can only be inferred from ecological studies on controls on mangrove distributions. Stratigraphic studies can also show long-term net sedimentation rates from either ^{14}C or shorter term ^{210}Pb and ^{137}Cs. The contribution to this from inorganic or organic sediment can be determined, but accretion cannot be distinguished from either shallow subsidence or compaction as can be done in the modern environment using a surface elevation table in combination with a marker horizon (Cahoon et al., 2002). The results from this technique, however, correspond well with radiocarbon dated long-term rates of sediment accretion in mangroves (Ellison and Stoddart, 1991; Ellison, 2005; Cahoon, 2006).

The link between long-term mangrove community change as determined from palaeoecology and short-term ecological change (Berger et al., 2008; Bosire et al., 2008; Komiyama et al., 2008; Krauss et al., 2008) will be monitoring of mangroves over time periods of decades, using standard techniques between sites (English et al., 1997). While such long-term monitoring of coral reefs is well under way by a number of agencies, there has been slow development of this in mangroves despite some well meaning initiatives (UNEP-IOC-WMO-IUCN, 1991; UNEP, 1994).

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References

Bartlett, A.S., Barghoorn, E.S., 1973. Phytogeographic history of the isthmus of Panama during the past 12,000 years (A history of vegetation, climate and sea level change). In: Graham, A. (Ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier, Amsterdam, pp. 203–299.

Behling, H., Cohen, M.C.L., Lara, R.J., 2001. Studies on Holocene mangrove ecosystem dynamics of the Bragança Peninsula in north-eastern Pará, Brazil. Palaeogeogr. Palaeoclimatology 167, 225–242.

Behling, H., Cohen, M.C.L., Lara, R.J., 2004. Late Holocene mangrove dynamics of Marajó Island in Amazonia, northern Brazil. Veg. Hist. Archeobot. 13, 73–80.

Benninghoff, W.S., 1962. Calculation of pollen and spores density in sediments by addition of exotic pollen in known quantities. Pollen Spores 4, 332–333.

Berdin, R.D., Siringan, F.P., Maeda, Y., 2003. Holocene relative sea-level changes and mangrove response in southwest Bohol, Philippines. J. Coast. Res. 19, 304–313.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Berry, E.W., 1914. Upper Cretaceous and Eocene floras of South Carolina and Georgia. U.S. Geol. Surv. Prof. Paper, p. 84.

Bloom, A.L., 1970. Paludal stratigraphy of Truk, Ponape, and Kusaie, Eastern Caroline Islands. Geol. Soc. Am. Bull. 81, 1904–1985.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Cahoon, D.R., Lynch, J.C., 1997. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, U.S.A. Mangr. Salt Marshes 1, 173–186.

Cahoon, D.R., Lynch, J.C., Perez, B.C., Segura, B., Holland, R., Stelly, C., Stephenson, G., Hensel, P., 2002. High precision measurement of wetland sediment elevation: II. The rod surface elevation table. J. Sed. Res. 72, 734–739.

Cahoon, D.R., 2006. High-resolution global assessment of mangrove responses to sea-level rise: a review. In: Gilman, E. (Ed.), Proc. Sympos. on Mangrove Responses to Relative Sea-Level Rise and Other Climate Change Effects, 13 July 2006. The Society of Wetland Scientists 27th International Conference. Western Pacific Regional Fishery Management Council, Honolulu, USA, pp. 9–17.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Chapman, V.J., 1975. Mangrove biogeography. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proc. Internat. Sympos. Biol. Manag. Mangr., vol. 1, Gainesville, University of Florida, pp. 3–21.

Chapman, V.J., 1976. Mangrove Vegetation. J. Cramer, Vaduz.

Chappell, J.M.A., Grindrod, J., 1985. Pollen analysis: a key to past mangrove communities and successional changes in North Australian coastal environments. In: Bardsley, K.N., Davie, J.D.S., Woodroffe, C.D. (Eds.), Coasts and Tidal Wetlands of the Australian Monsoon Region. Australian National University, Canberra, pp. 225–236.

Cohen, A.D., Spackman, W., 1977. Phytogenic organic sediments and sedimentary environments in the Everglades–mangrove complex. Palaeontograph. Abt B 10–144.

Cohen, M.C.L., Souza Filho, P.W.M., Lara, R.J., Behling, H., Angulo, R.J., 2005. A model of Holocene mangrove development and relative sea-level changes on the Bragança Peninsula (northern Brazil). Wetlands Ecol. Manag. 13, 433–443.

Dahdouh-Guebas, F., Koedam, N., 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: A review. Aquat. Bot. 89, 80–92.

De Boer, N.P., Van Der Hammen, T., Wijmstra, T.A., 1965. A palynological study on the age of some borehole samples from the Amazon delta area, N.W. Brazil. Geologie en Mijnbouw 44, 254–258.

DeLaune, R., Patrick Jr., W., Buresh, R., 1978. Sedimentation rates determined by ^{137}Cs dating in a rapidly accreting salt marsh. Nature 275, 532–533.

Donnelly, J., Bertness, M., 2001. Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. Proc. Natl. Acad. Sci. 98, 14218–14223.

Duke, N.C., 2002. Global distribution and genetic discontinuities of mangroves—emerging patterns in the evolution of Rhizophora. Trees Struct. Funct. 16, 65–79.

Duke, N.C., Meynecke, J.-O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Ellison, A.M., Farnsworth, E.J., Merkt, R.E., 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. Global Ecol. Biogeogr. 8, 95–115.

Ellison, J.C., 1989. Pollen analysis of mangrove sediments as a sea level indicator: Assessment from Tongatapu, Tonga. Palaeogeogr., Palaeoclimatol. 74, 327–341.

Ellison, J.C., 1991. The Pacific palaeogeography of Rhizophora mangle L. (Rhizophoraceae). Bot. J. Linn. Soc. 105, 271–284.

Ellison, J.C., 1993. Mangrove retreat with rising sea-level, Bermuda. Estuar. Coast. Shelf Sci. 37, 75–87.

Ellison, J.C., 1994. Palaeo-lake and swamp stratigraphic records of Holocene vegetational and sea-level changes, Mangaia, Cook Islands. Pacif. Sci. 48, 1–15.

Ellison, J.C., 1995. Systematics and taxonomy of Pacific Island mangroves. In: Maragos, J.E., Peterson, M.N.A., Eldredge, L.G., Bardach, J.E. (Eds.), Marine and Coastal Biodiversity in the Tropical Island Pacific Region: I. Species Systematics and Information Management Priorities. East West Center, Honolulu.

Ellison, J.C., 1996. Pollen evidence of Late Holocene mangrove development in Bermuda. Global Ecol. Biogeogr. 5, 315–326.

Ellison, J.C., 2005. Holocene palynology and sea-level change in two estuaries in Southern Irian Jaya. Palaeogeogr. Palaeoclimatol. 220, 291–309.

English, S., Wilkinson, C., Baker, V., 1997. Manual for Survey of Tropical Marine Resources, second ed. Australian Institute of Marine Science, Townsville.

Erdtman, O.E.G., 1969. Handbook of Palynology. Hafner, New York.

Faegri, K., Iversen, J., 1975. Textbook of Pollen Analysis. Hafner, New York.

Flenley, J., 1979. Vegetational history of equatorial mountains. Prog. Phys. Geog. 3, 488–509.

Fujimoto, K., 1997. Mangrove habitat evolution related to Holocene sea-level changes on Pacific islands. Tropics 6, 203–213.

Furukawa, K., Wolanski, E., 1996. Sedimentation in mangrove forests. Mangr. Salt Marshes 1, 3–10.

Furukawa, K., Wolanski, E., Mueller, H., 1997. Currents and sediment transport in mangrove forests. Estuar. Coast. Shelf Sci. 44, 301–310.

Germeraad, J.H., Hopping, C.A., Muller, J., 1968. Palynology of tertiary sediments from Tropical Areas. Rev. Palaeobot. Palyno. 6, 189–348.

Gilman, E., Ellison, J.C., McMurtry, G.M. (under review). Accretion in American samoa mangroves based on ^{137}Cs and excess ^{210}Pb activity depth profiles: implications for mangrove vulnerability to relative sea-level rise. Estuar. Coast. Shelf Sci.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Graham, A., Jarzen, D.M., 1969. Studies in Neotropical paleobotany. I: the Oligocene communities of Puerto Rico. Ann. Missouri Bot. Garden 56, 308–357.

Graham, A., 1995. Diversification of Gulf Caribbean mangrove communities through Cenozoic time. Biotropica 27, 17–20.

Grimm, E., 1988. Data analysis and display. In: Huntley, B., Webb, T. (Eds.), Vegetation History. Kluwer, Dordrecht.

Grindrod, J., 1985. The palynology of mangroves on a prograded shore, Princess Charlotte Bay, N. Queensland, Australia. J. Biogeogr. 12, 323–348.

Grindrod, J., 1988. The palynology of mangrove and saltmarsh sediments, particularly in Northern Australia. Rev. Palaeobot. Palyno. 55, 229–245.

Grindrod, J., Rhodes, E.G., 1984. Holocene sea level history of a tropical estuary: Missionary Bay, north Queensland. In: Thom, B.G. (Ed.), Coastal Geomorphology in Australia. Academic Press, New York, NY, pp. 151–178.

Hadac, E., 1976. Species diversity of mangrove and continental drift. Folia Geobot. Phytotx. 11, 213–216.

Hamilton, L.S., Snedaker, S.C., 1984. Handbook for Mangrove Area Management. East-West Center, IUCN and UNESCO, Honolulu.

Hansen, A., Neilson, R., Dale, V., Flather, C., Iverson, L., Currie, D., Shafer, S., Cook, R., Bartlein, P., 2001. Global change in forests: responses of species, communities and biomes. Bioscience 51, 765–779.

Hansen, L.J., Biringer, J., 2003. Building resistance and resilience to climate change. In: Hansen, L.J., Biringer, J.L., Hoffmann, J.R. (Eds.), Buying Time: A User's Manual for Building Resistance and Resilience to Climate Change in Natural Systems. Martin Hiller, Washington DC, pp. 9–14.

Haseldonckx, P., 1977. The palynology of a Holocene marginal peat swamp environment in Johore, Malaysia. Rev. Palaeobot. Palynol. 24, 238–277.

Kennett, J.P., Stott, L.D., 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. Nature 353, 225–229.

Kershaw, A.P., 1976. A late Pleistocene and Holocene pollen diagram from Lynch's Crater, north-east Queensland, Australia. New Phytol. 77, 469–498.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Ladd, H.S., 1965. Tertiary fresh-water mollusks from Pacific Islands. Malacolog 2, 189–197.

Langenheim, J.H., Hackner, B.L., Bartlett, A., 1967. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. Bot. Museum Leaflets 21, 289–324.

Laeyendecker- Roosenburg, D.M., 1966. A palynological investigation of some archaeologically interesting sections in Northwestern Surinam. Leidse Geologische Mededelingen 38, 31–36.

Leopold, E.B., 1969. Miocene pollen and spore flora of Enewetok Atoll, Marshall Islands. U.S. Geol. Surv. Prof. Paper 260-II.

Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. 5, 39–64.

Lynch, J., Meriwether, J., McKee, B., Vera-Herrera, F., Twilley, R., 1989. Recent accretion in mangrove ecosystems based on ^{137}Cs and ^{210}Pb. Estuaries 12, 284–299.

Middleton, G.V., 1973. Johannes Walther's Law of the correlation of facies. Geol. Soc. Am. Bull. 84, 979–988.

Mildenhall, D.C., 1994. Early to mid Holocene pollen samples containing mangrove pollen from Sponge Bay, East Coast, North Island, New Zealand. J. R. Soc. N.Z. 24, 219–230.

Mildenhall, D.C., Brown, L.J., 1987. An early Holocene occurrence of the mangrove Avicennia marina in Poverty Bay, North Island, New Zealand: it climatic and geological implications. N.Z. J. Bot. 25, 281–294.

Muller, J., 1959. Paleontology of recent Orinoco Delta and shelf sediments. Micropaleontol. 5, 1–32.

Muller, J., Caratini, C., 1977. Pollen of Rhizophora (Rhizophoraceae) as a guide fossil. Pollen Spores 19, 361–389.

Muller, J., 1964. A palynological contribution to the history of the mangrove vegetation in Borneo. In: Cranwell, L.M. (Ed.), Ancient Pacific Floras. University of Hawaii Press, Honolulu.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Parkinson, R.W., 1989. Decelerating Holcene sea-level rise and its influence on Southwest Florida coastal evolution: A transgressive/ regressive stratigraphy. J. Sed. Petrol. 59, 960–972.

Plaziat, J.-C., Cavagnett, C., Koeniguer, J.-C., Baltzer, F., 2001. History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. Wetlands Ecol. Manag. 9, 161–179.

Roeleveld, W., 1969. Pollen analysis of two sections in the young coastal plain of Surinam. Geol. Mijnbouw 48, 215–224.

Ross, M.S., O Brien, J.J., Sternberg, L.D., 1994. Sea level rise and the reduction of pine forests in the Florida keys. Ecol. Appl. 4, 144.

Rull, V., 1998. Middle Eocene mangroves and vegetation changes in the Maracaibo Basin, Venezuela. Palaios 13, 287–296.

Scholl, D.W., 1964. Recent sedimentatary record in mangrove swamps and rise in sea level over the south- west coast of Florida. Mar. Geol. 2, 343–364.

Scholl, D.W., Craighead, F.C., Stuiver, M., 1969. Florida submergence curve revised: its relation to coastal sedimentation rates. Science 163, 562–564.

Scholl, D.W., Stuiver, M., 1967. Recent submergence of southern Florida: a comparison with adjacent coasts and other eustatic data. Geol. Soc. Am. Bull. 78, 437–454.

Saenger, P., 1998. Mangrove vegetation: an evolutionary perspective. Marine Freshwater Res. 49, 277–286.

Shackleton, N.J., Opdyke, N.D., 1973. Oxygen isotope and palaeo-magnetic stratigraphy of the Equatorial Pacific core V28-238. oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year scale. Quat. Res. 3, 39–55.

Semeniuk, V., 1980. Mangrove zonation along an eroding coastline in King Sound, North-Western Australia. J. Ecol. 68, 789–812.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, K., McCormac, G., Plicht, J., Spurk, M., 1998. INTCAL98 Radiocarbon Age Calibration. Radiocarbon 40, 1041–1083.

Triest, L., 2008. Molecular ecology and biogeography of mangrove trees towards conceptual insights on gene flow and barriers: A review. Aquat. Bot. 89, 138–154.

UNEP-IOC-WMO-IUCN, 1991. Meeting of experts on a long-term global monitoring system of coastal and nearshore phenomena, pilot projects on mangroves and coral reefs. Intergovernmental Oceanographic Commission Report of Meetings of Experts and Equivalent Bodies, vol. 69.

UNEP, 1994. Assessment and monitoring of climatic change impacts on mangrove ecosystems. UNEP Regional Seas Reports and Studies No. 154.

Vishnu-Mittre, Guzder, S., 1973. Stratigraphy and palynology of the mangrove swamps of Bombay. Paleobotanist 22, 111–117.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Westgate, J.W., Gee, C.T., 1990. Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. Palaeogeogr. Palaeoclimatol. 78, 163–177.

Wijmstra, T.A., 1969. Palynology of the alliance well. Geol. Mijnbouw 48, 125–134.

Woodroffe, C.D., 1995. Response of tide dominated mangrove shorelines in Northern Australia to anticipated sea-level rise. Earth Surf. Proc. Landforms 20, 65–85.

Woodroffe, C.D., Thom, B.G., Chappell, J., 1985. Development of widespread mangrove swamps in mid- Holocene times in northern Australia. Nature 317, 711–713.

Woodroffe, C.D., Mulrennan, M.E., 1993. Geomorphology of the Lower Mary River Plains, Northern Territory. North Australia Research Unit, Darwin.

Wooller, M.J., Behling, H., Smallwood, B.J., Fogel, M., 2004. Mangrove ecosystem dynamics and elemental cycling at Twin Cays, Belize, during the Holocene. J. Quat. Sci. 19, 703–711.

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Review

Environmental drivers in mangrove establishment and early development: A review

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Abstract

Mangroves have a global distribution within coastal tropical and subtropical climates, and have even expanded to some temperate locales. Where they do occur, mangroves provide a plethora of goods and services, ranging from coastal protection from storms and erosion to direct income for human societies. The mangrove literature has become rather voluminous, prompting many subdisciplines within a field that earlier in the 20th century received little focus. Much of this research has become diffuse by sheer numbers, requiring detailed syntheses to make research results widely available to resource managers. In this review, we take an inclusive approach in focusing on eco-physiological and growth constraints to the establishment and early development of mangrove seedlings in the intertidal zone. This is a critical life stage for mangroves, i.e., the period between dispersal and recruitment to the sapling stage. We begin with some of the research that has set the precedent for seedling-level eco-physiological research in mangroves, and then we focus on recent advances (circa. 1995 to present) in our understanding of temperature, carbon dioxide, salinity, light, nutrient, flooding, and specific biotic influences on seedling survival and growth. As such, we take a new approach in describing seedling response to global factors (e.g., temperature) along with site-specific factors (e.g., salinity). All variables will strongly influence the future of seedling dynamics in ways perhaps not yet documented in mature forests. Furthermore, understanding how different mangrove species can respond to global factors and regional influences is useful for diagnosing observed mortality within mangrove wetlands, managed or natural. This review provides an updated eco-physiological knowledge base for future research and reforestation activity, and for understanding important links among climate change, local physico-chemical condition, and establishment and early growth of mangrove seedlings.

Keywords: Biotic effect; CO_2; Ecophysiology; Flooding; Global climate change; Growth; Light; Nutrient; Salinity; Sea-level rise; Temperature

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1. Introduction

Globally, mangroves are generally undervalued, overexploited, and poorly managed (Ewel et al., 1998a). Yet, their importance to humans, wildlife, and global carbon balance is paramount (Walters et al., 2008; Nagelkerken et al., 2008; Kristensen et al., 2008). Human activities have destroyed 35% of the world' mangrove forests over the last two decades (Valiela et al., 2001), and mangrove conservation and sustainable use as a zone of critical transition between land and sea needs to be better appreciated (Ewel et al., 2001; Saenger, 2002). Such human impacts and global change have prompted worldwide scientific interest in understanding the ecology and eco-physiological requirements of mangrove establishment, persistence, growth, and development (Robertson and Alongi, 1992; Kathiresan and Bingham, 2001; Saenger, 2002). The literature is vast, so an updated review of experimental studies may be the only effective way for coastal managers to understand how mangrove seedlings respond eco-physiologically to the many natural, anthropogenic, and global-change-induced factors worldwide.

In this review, we focus on eco-physiological and growth constraints to the establishment and early development of mangrove seedlings. We thus describe a critical life stage for mangroves. Our focus generally assumes that reproductive propagules have escaped losses from pre-dispersal herbivory and dispersal, and that once a seedling becomes rooted, survives, and develops to the sapling stage (approx. 1 m tall), that it has successfully established. We begin with some of the past research that has set the precedent for seedling-level, eco-physiological theory in mangroves that is not specifically addressed in subsequent sections, and then we focus on recent advances (circa. 1995) in our understanding of how temperature, carbon dioxide (CO_2), salinity, light, nutrients, flooding, and specific biotic entities affect early seedling establishment, growth, and eco-physiological proficiency.

2. Eco-physiological paradigms

Explaining potential eco-physiological responses of mangroves to salinity, flooding, and light were important contributions of past reviews (Ball, 1986, 1988a, 1998; Smith et al., 1989; Popp et al., 1993). In fact, many hypotheses have developed directly from those reviews and are still being tested by contemporary science programs. For this reason, we begin this review by summarizing five central paradigms that will not be discussed specifically in subsequent sections, but that are often used to interpret experimental results of studies on mangrove seedlings during establishment and early developmental phases.

2.1. The lack of a functional understory in many mangrove forests

The mangrove forest floor is often covered with seedlings and saplings of overstory species; however, there is a notable lack of herbaceous, shrub, and vine species in many forests. Chapman (1976) and Janzen (1985) made official note of this phenomenon and were puzzled that mangrove trees evolved to persist in the intertidal zone along multiple taxonomic lineages, yet herbs, shrubs, and vines had not. Janzen (1985) suggested that the most probable reason for this might simply be that plants were not able to garner enough carbohydrates from photosynthesis while being shaded to meet the metabolic demands of reproduction in saline soils.

Lugo (1986) argued that a functional understory does exist in high rainfall mangroves, and cited Chapman (1976) who listed many species of vines, herbs, ferns, and palms that occur in landward edge mangrove forests. These species begin to appear when soil salinity decreases. Lugo also suggested a modification of Janzen's ideas to include other stressors such as hydrogen sulfide, low oxygen, and low nutrients, which might be as important as light. Generally, however, Janzen (1985) and Lugo (1986) both agreed that the combination of stressors is prohibitive to reproduction in the mangrove understory.

Corlett (1986) suggested that tidal flooding, not salt, caused some freshwater forested wetlands at similar latitudes to lack an understory. Finally, Snedaker and Lahmann (1988) agreed with Lugo (1986) in suggesting that some factor other than salinity and light must be responsible, but that where the understory did exist along a landward edge, for example, circumstances were atypical. This discussion ends with the notion that ''the intertidal environment has largely precluded the evolution of: (1) intertidal-halophytic adaptations in shade-tolerant terrestrial or freshwater aquatic species, (2) true shade-tolerance in intertidal halophytes, or (3) both characteristics in shade-intolerant plants'' (p. 313, Snedaker and Lahmann, 1988).

2.2. Inundation classifications

Much of the literature on establishment and early development of mangroves have either ignored the effects of tidal flooding within laboratory settings or have failed to quantify tidal inundation in the field. However, Watson (1928) defined the importance of tidal flooding in mangroves many years prior to most experimental investigations. In a general sense, inundation classes were useful for describing the distribution patterns of 17 mangrove species in Malaysia. Classifications included forests with inundation by all high tides, inundation by medium high tides, inundation by normal high tides, inundation by spring tides, and occasional inundation by exceptional or equinoctial tides (Watson, 1928). Different species of mangroves tended to grow among distinctive zones, and although these zones have characteristic hydroperiods, many mangrove species are capable of colonizing a range of inundation frequencies. What was important, however, was that segregation by flood state did occur naturally.

Chapman later applied this classification to south Florida mangroves where species diversity is considerably lower (Chapman, 1976). There, *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus* tended to transgress the continuum from inundation by spring tides to inundation by exceptional events in that respective order (Chapman, 1976). Explanations for these distributional patterns, or ''zonation'', have since developed into a hypothesis rich debate, but many proposed factors are intricately linked to the depth, duration, and frequency of tidal flooding inherent to Watson's classifications.

2.3. Salinity tolerance, zonation, and biomass allocation

Interrelatedness of tidal flooding with salinity, fertility, and soil saturation influences zonation in mangroves on a site-specific basis (Ball, 1988a). Indeed, mangrove forests often segregate as distinctive bands of species (Saenger et al., 1977). From an eco-physiological perspective, species may overlap considerably in their range of tolerances to environmental factors, flooding or otherwise (Ball, 1988a).

Ball (1988a) described this overlap by first making the observation that mangrove species vary widely in their abilities to cope with salinity and rarely partition within a narrow functional niche. Because the mangrove environment is so dynamic, natural selection has affected extensions in the ranges of species tolerance as opposed to fine-tuning this response (Ball, 1988a). What is left in many mangrove environments are species with slower growth rates under a wide range of conditions, thus maximizing coexistence under moderate stress levels (Fig. 1).

Zonation theory in mangroves has a rich experimental history (Smith, 1992; but see Ellison et al., 2000), and includes hypotheses ranging from tidal sorting (Rabinowitz, 1978a,b; but see Sousa et al., 2007) to differential predation by crabs (Smith, 1987a,b,c; and more recently Sousa and Mitchell, 1999; Allen et al., 2003; Dahdouh-Guebas et al., 2002, 2004, among others). Ball (1988a), however, focuses on the evolutionary tolerance of established seedlings, saplings, and trees, which serves to explain many situations where zonation does appear.

2.4. Interrelatedness of nutrient enrichment, growth, and herbivory

Slow growth is often characteristic of plants in resource-limited environments as a potential tradeoff to anti-herbivore defense (Chapin et al., 1987). Small trees in stunted *R. mangle* forests on Caribbean islands and elsewhere have characteristics

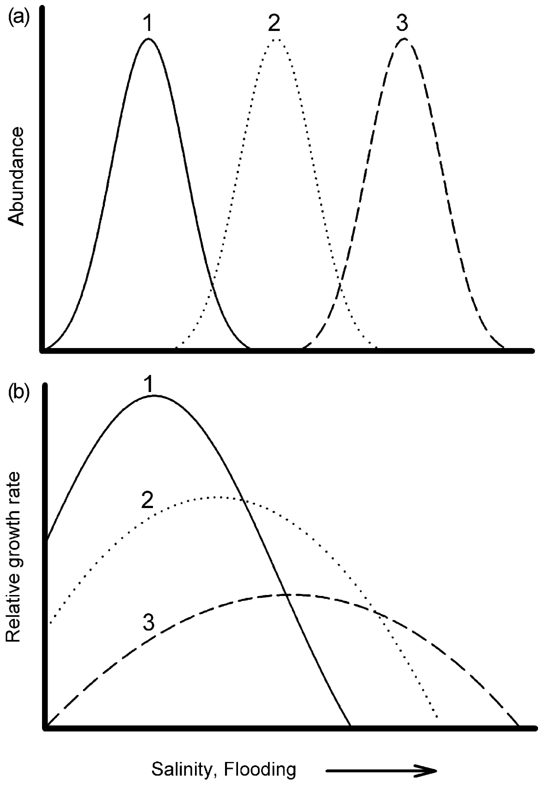

Fig. 1. Hypothetical response of three co-occurring mangrove species varying in salinity and flood tolerance (after Ball, 1988a). The top graph (a) depicts relative species abundance at a particular salinity or flood regime, while the bottom graph (b) indicates idealized ranges of physiological growth optima for species 1, 2, and 3 at specific salinity or flood regimes.

associated with resource limitation, including a small stature and schlerophyllous leaves. However, these sites, and many others globally, have additional stress gradients to consider. How, for example, does herbivory affect the host plant's condition along different nutrient, flood, and salinity gradients, and how are rates of herbivory affected by the host plant's condition?

A comprehensive, manipulative field experiment was designed in resource-limited settings to address these questions (Feller, 1995). Feller (1995) fertilized stunted trees with NPK, P, or N along a water depth and tidal elevation gradient and tracked many growth variables over two years. Growth was enhanced greatly by NPK and P fertilization, but was unaffected by N fertilization relative to controls for nearly all variables. Fertilization also enhanced the activity of specialist insects that feed on apical buds or bore into the stem, but had no effect on generalist folivores. Accordingly, leaf schlerophylly was found to be a strategy for coping with nutrient limitation in these environments rather than for herbivore defense. Fertilization of trees with NPK and P actually stimulated the production of less schlerophyllous leaves that were not nearly as tough as N-fertilized and control leaves after only 2 years (Feller, 1995).

Phosphorus has been described as a limiting nutrient controlling growth and productivity of many mangrove systems (Koch and Snedaker, 1997; Sherman et al., 1998; Chen and Twilley, 1999). Tradeoffs to herbivory may also be similar in other mangrove forests worldwide, with the activities of specialist herbivores increasing proportional to site fertility and the activities of generalist folivores remaining constant at all canopy levels (Feller, 1995).

2.5. Geomorphological classification

Mangrove scientists have often been limited in their abilities to make comparisons among the incredible variety of geologic settings, hydrological fluxes, and geographical locations for which mangrove field studies are conducted. For south Florida, Lugo and Snedaker (1974) developed a common metric based upon the premise that geophysical processes and landscape position dictate the basic patterns of forest structure (Twilley, 1998), and proposed to separate mangroves into overwash islands, fringe, riverine, basin, hammock, and scrub forests. These ecological types differ predictably by soil type, salinity, and hydroperiod (Odum et al., 1982), and have been used to partition the functional description of many mangrove forests throughout the world.

However, there was a need to split these designations further in order to be more inclusive of global mangrove settings for which a more comprehensive ecogeomorphological classification scheme was needed (Woodroffe, 1992; Twilley et al., 1998). For this, segregation is first made by geomorphic type as delta, lagoon, delta/lagoon, or estuary mangroves based upon the degree of terrigenous input and position of the mangrove forest relative to this input (Fig. 2). The classification scheme predicts that forcing functions will act differentially based upon geomorphology and will lead to discrepancies in total energy

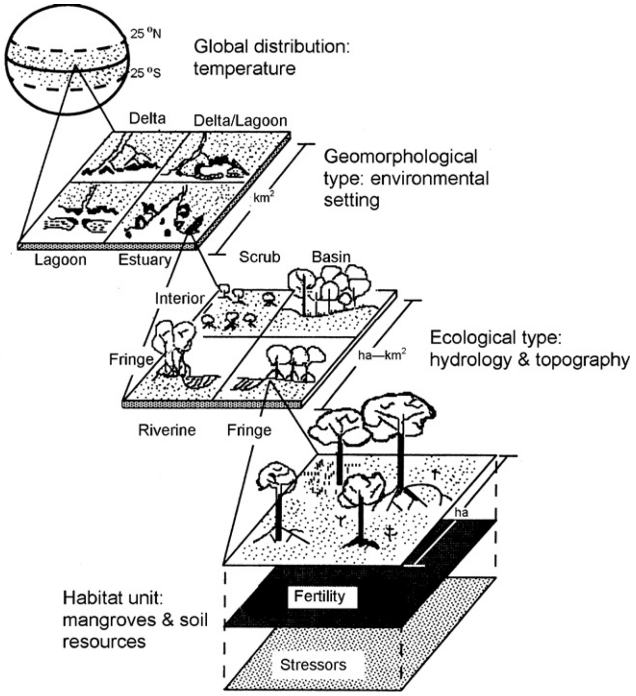

Fig. 2. Hierarchical classification system (ecogeomorphology) for use among different mangrove ecosystems worldwide, whereby function is based upon geomorphological development, ecological factors, site fertility, salinity gradients, and flood regimes (after Twilley et al., 1998).

flow potential for the specific mangrove location (Twilley, 1995). For example, this would explain why a fringe forest on a Micronesian island may respond differently to sea-level rise than a fringe forest in Panama even though latitudes may be similar. Ecological classifications (sensu Lugo and Snedaker, 1974) and a description of soil resources and stress gradients are then superimposed upon geomorphological setting to produce an overall classification scheme robust to the many conditions of mangrove forests globally (Fig. 2). The potential for mangrove seedling establishment and early development, hence, is similar within a given site ecogeomorphological class.

3. Temperature

Temperature is a major factor that varies greatly within forests, between forest types, and geographically across the distributional range of mangrove vegetation, and can therefore have tremendous impact on seedling establishment. Mangroves may encounter either high or low temperature extremes, although most work has emphasized the latter.

3.1. Temperature extremes

Low temperature is widely regarded as the primary control on the latitudinal limits of mangroves globally (Lugo and Zucca, 1977; Tomlinson, 1986; Duke et al., 1998). Mangrove vegetation is essentially tropical and its distribution is constrained by sensitivity to freezing temperatures (Norman et al., 1984; Sherrod and McMillan, 1985; McMillan and Sherrod, 1986; Sherrod et al., 1986; Schaeffer-Novelli et al., 1990; Kao et al., 2004; Stevens et al., 2006; Stuart et al., 2007). The distributional limits of mangroves generally coincide with the 20 °C winter isotherm of seawater (Duke et al., 1998). Northernmost populations occur at ~32°N latitude (Bermuda, Japan) and southernmost populations occur at ~37–38°S latitude (Australia and New Zealand).

Reviews of physiological effects of chilling and freezing temperatures on plants (Larcher, 2001) provide a background for understanding effects on mangrove establishment and early development. In increasing order of impact to plants, low temperatures may: (1) increase the rigidity of biomembranes and increase the energy required for activating biochemical reactions, (2) cause chilling injury (as a consequence of lesions in biomembranes and interruption of energy supply to cells), or (3) freeze plant tissues, leading to vascular embolism, dehydration, or cellular rupture. The threshold temperature range for tropical trees (leaf tissue) is +5 to −2 °C.

Differential temperature sensitivity can be seen in mangroves. For example, *A. germinans* is widely regarded to be less sensitive to chilling temperatures than *R. mangle* (McMillan and Sherrod, 1986; Sherrod et al., 1986). Propagules of *R. mangle* that establish naturally or are planted in southern Texas cannot survive winter freezes, whereas *A. germinans* can (Sherrod et al., 1986). *Avicennia* spp. are typically found at the extreme latitudinal limits of mangrove distribution, e.g., *A. germinans* in North America (~32°N) (Sherrod and McMillan, 1985) and *A. marina* in Australia and New Zealand (~37°S) (Sakai and Wardle, 1978; Duke et al., 1998). Other work shows an exponential decrease in the numbers of mangrove species with decreasing air temperatures in northeastern Asia (Hsueh and Lee, 2000).

3.2. Cold tolerance

Among the earliest studies to document freeze effects on mangroves was an investigation carried out at Seahorse Key, Florida (USA) on the Gulf of Mexico (29°08′N) (Lugo and Zucca, 1977). Inventories of frost damage to mature *A. germinans* were conducted following a record freeze (−2.7 °C), but also provided some qualitative observations for seedlings. Those seedlings growing in open areas were more negatively affected by frost than those growing intermixed with salt marsh, with the exception of mangroves that were taller than the salt marsh canopy. Also, seedlings growing under the mangrove canopy appeared to be unaffected.

Differences in cold tolerance among species are hypothesized to explain the more restricted distributions of *R. mangle* and *L. racemosa* in the Gulf of Mexico compared to *A. germinans* (Sherrod and McMillan, 1985). Early field and laboratory experiments support this hypothesis with respect to *R. mangle*. Seedlings transplanted from northern Florida to South Padre Island and Rio Grande, Texas (USA) could not survive sub-freezing temperatures at these locations (Sherrod et al., 1986). Field observations of *A. germinans* in Texas, Louisiana, and Florida indicated that this species can survive temperatures as low as −4 °C, but mature trees suffer near-total mortality at temperatures below −6.7 °C (Stevens et al., 2006). In New Zealand, *A. marina* (woody shoots) was unable to survive temperatures to −3 °C (Sakai and Wardle, 1978).

Other work focused on within-species variation in chilling sensitivity of mangroves (Markley et al., 1982; Norman et al., 1984; McMillan and Sherrod, 1986; Sherrod et al., 1986). Rooting of *A. germinans* from the coast of Texas was examined in the greenhouse over a range of temperatures, and seedlings at or below 15 °C failed to root (McMillan, 1971). Propagules and rooted seedlings of *A. germinans*, *R. mangle*, and *L. racemosa* collected over a latitudinal range from 17°45′N to 27°50′N were subjected to chilling temperatures (2–4 °C for 3–6 days) in the laboratory (Markley et al., 1982). Chilling tolerance of all three species appeared to vary with latitude, with material of more tropical origin showing greater sensitivity to low temperature. Seedlings and older specimens of *R. mangle* from more northern latitudes exhibited less physiological dysfunction (Sherrod et al., 1986).

The results of several chilling experiments (Markley et al., 1982; McMillan and Sherrod, 1986; Sherrod et al., 1986) were combined and analyzed statistically to determine if chilling sensitivity of propagules or seedlings of *A. germinans*, *L. racemosa*, and *R. mangle* varied significantly with latitude of the source material. Percent mortality of propagules and percent of rooted seedlings exhibiting leaf injury increased with decreasing latitude of source material, but the pattern did not differ among species (no species by latitude interaction ($P > 0.05$)) (Fig. 3). However, mortality of propagules differed

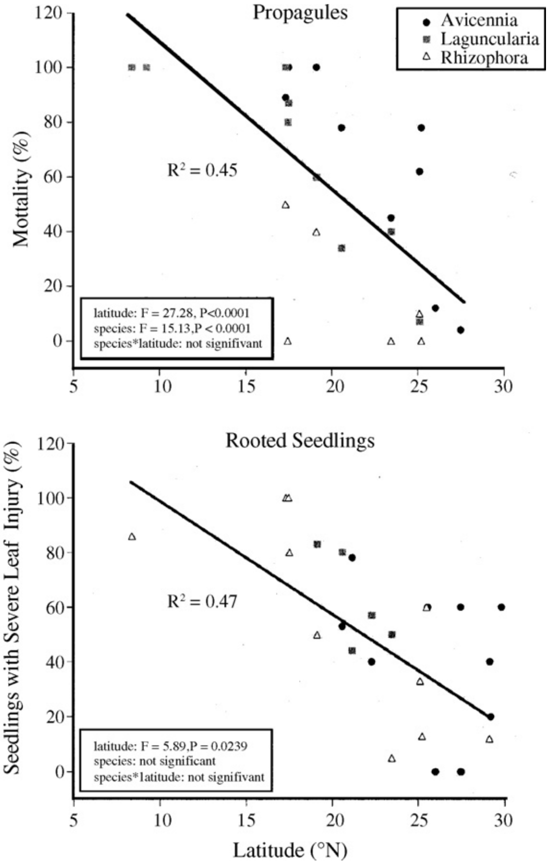

Fig. 3. Effects of mangrove species and geographic source on propagule mortality (upper panel) and percentage of rooted seedlings with severe leaf injury (lower panel) after exposure to chilling temperatures (2–4 °C for 5–6 days). Data from Markley et al. (1982), McMillan and Sherrod (1986), and Sherrod et al. (1986).

significantly among species, averaged across latitude: *A. germinans* (67%), *L. racemosa* (68%), and *R. mangle* (17%). These results indicate differences with latitudinal source, but cannot distinguish whether this variation is due to phenotypic plasticity or to genetic differences among mangrove populations.

3.3. Heat tolerance

Although less well studied, high temperatures can greatly influence the survival and growth of mangrove seedlings. Solar radiation varies spatially across mangrove forests, e.g., with degree of canopy development or disturbance frequency and severity. Incident light affects soil and water temperatures, which may greatly increase plant respiration or cause direct damage to sensitive tissues. High temperatures may cause one or more effects, including (1) limit physiological processes through enzyme denaturation or membrane damage, or (2) cause death of tissues or the whole plant, reducing its competitive vigor or eliminating it from a particular niche. Some symptoms of high-temperature injury are (1) chlorotic mottling of leaves, fruits, etc., (2) appearance of necrotic lesions, particularly on stems and hypocotyls (part of seedling below attachment of cotyledons), and (3) death. Plant organs usually suffer heat damage at temperatures between 40 and 55 °C. Heat sensitivity is also correlated with the stage of growth, i.e., actively growing tissues (meristems) or seedlings are more susceptible to heat than mature tissues.

In general, plants avoid heat damage by several mechanisms, which are observed in mangroves: heliotropism (reorientation of leaves to minimize interception of incident radiation) (Ball et al., 1988), increased reflectance properties of the leaf to decrease leaf temperature (e.g., hairs on abaxial leaf surfaces of *A. germinans* or the ‘‘silver’’ variety of *C. erectus*), dissipation of heat by evaporative cooling during transpiration, and establishment in cool habitats (shade, water). Plant tissues may experience high temperatures, but exhibit protoplasmic tolerance, which is genetically determined and varies among plant species (Larcher, 2001).

Rooting of *A. germinans* seedlings from coastal Texas was inhibited at 37 °C, whereas 10-min exposures to 43 °C were not lethal (McMillan, 1971). Forty-eight-hour exposures to 39–40 °C caused death and decay of rooted seedlings (prior to epicotyl expansion), but the same treatment did not damage seedlings with shoots and leaves (McMillan, 1971). One study found that root respiration rates of *R. mangle*, *A. germinans*, and *L. racemosa* seedlings increased linearly with temperature (20–45 °C), and their respective Q_{10} values differed significantly over the temperature range of 20–30 °C (1.5, 1.7, and 2.7), but were similar at 30–40 °C (1.3, 1.5, and 1.5) (McKee, 1996). Data indicated a major change in root metabolism or membrane integrity near 30 °C for all three species, and it was clear that small changes in soil temperature could have a potentially large effect on relative growth of mangrove seedlings.

3.4. Synthesis of temperature studies

Detailed information about temperature effects on early growth and physiology of mangroves is essentially lacking, and this information gap will greatly limit predictions of future effects of climate change on mangroves and interactions with subtropical and temperate vegetation. Temperature extremes are important in determining distributional limits of mangroves, but the physiological mechanisms responsible for reduced growth and mortality are not fully understood. Future work should endeavor to elucidate these mechanisms and to identify temperature thresholds for important species. Most work has emphasized low temperature stress, but high temperature extremes may be important, especially in arid habitats and in disturbed areas. Limited work suggests interspecific differences in temperature tolerance, but few mechanisms (e.g., biochemical components, xylem vessel anatomy, root respiration) have been examined experimentally. Similarly, population variation in low temperature sensitivity has been reported for a few mangrove species, but further work is needed to confirm ecotypic differentiation in these and other species. Finally, no work has examined interaction of temperature with other important growth-limiting factors such as flooding, salinity, nutrients, or CO_2. Information about multi-stress interactions is necessary to make accurate predictions of mangrove seedling response to temperature.

4. Atmospheric CO_2 concentration

4.1. Photosynthesis and growth

Concentrations of atmospheric CO_2 have increased from 280 parts per million (ppm) in pre-industrial times to over 380 ppm today and are predicted to double over the next 50 years (IPCC, 2001). CO_2 enrichment may alter primary productivity of mangrove ecosystems due to enhanced net photosynthesis and photosynthetic water use efficiency (PWUE: carbon gain per unit of water lost) within certain ranges (Bazzaz, 1990; Urban, 2003). Studies have revealed increases in net photosynthetic rates with increases in CO_2 concentrations between 200 and 600 ppm with eventual saturation at concentrations of about 1000 ppm.

In addition to direct effects on assimilation rates, CO_2 concentrations also influence stomatal regulation of water loss. Under elevated CO_2, many species reduce their stomatal aperture and increase their PWUE. Response to CO_2, however, is further controlled by other growth-limiting factors such as nutrient availability and occurrence of stress factors such as salinity and flooding. The more nutrients are supplied to seedlings, the greater the absolute response to CO_2 enrichment. However, elevated CO_2 often reduces seedling demand for resources such as nutrients and water, so that relative growth responses to deficient conditions may be greater under elevated CO_2.

Another consideration relevant to early growth of mangroves is that the potential response to CO_2 is very dependent upon the activity of carbon sinks (growing tissues) and presence of carbon reserves (e.g., in cotyledons). A final consideration is that CO_2 enrichment typically alters leaf tissue quality, i.e., increases the concentration of nonstructural carbohydrates while decreasing tissue nitrogen (Poorter et al., 1997). This effect may result from several possible mechanisms, but the potential consequences for mangrove seedlings is to alter susceptibility to (1) photoinhibition (e.g., changes in photoprotective compounds, but see Section 6, below), and (2) herbivores (e.g., changes in tissue palatability).

4.2. Specific studies on mangroves

Thousands of articles describing plant species responses to elevated CO_2 have been published over the last decade, but only a handful have targeted mangrove species (Ball and Munns, 1992; Farnsworth et al., 1996; Ball et al., 1997; Snedaker and Araujo, 1998). All of the published work on CO_2 effects on mangroves have been conducted on isolated plants in greenhouse experiments or were based on short-term exposures to CO_2 (e.g., Snedaker and Araujo, 1998), both of which may overestimate potential growth responses and provides no information on how CO_2 may alter competition with other species or susceptibility to herbivores (e.g., through changes in tissue chemistry).

One species, *R. mangle*, was grown in ambient (350 $\mu l\,L^{-1}$, or ppm) and elevated (700 $\mu l\,L^{-1}$) atmospheric CO_2 concentrations for over 1 year in replicate greenhouses (Farnsworth et al., 1996). CO_2 enrichment significantly increased biomass, total stem length, branching, and total leaf area. Enhanced biomass under elevated CO_2 was attributed to higher relative growth rates and higher net assimilation rates. Photosynthesis rates were initially increased under elevated CO_2, but later declined and were not different from controls. Elevated CO_2 treatment also accelerated development of aerial prop roots and reproductive buds and increased foliar C:N ratios.

In another study, two Australian mangroves, *Rhizophora apiculata* and *R. stylosa* (3-month-old seedlings) were grown individually for 14 weeks in a multi-factorial experiment of salinity (25 and 75% seawater), humidity (43 and 85% relative humidity), and atmospheric CO_2 concentration (340 and 700 $\mu l\,L^{-1}$) (Ball et al., 1997). CO_2 had little effect on these species at higher salinity levels, but enhanced growth rates at low salinity, particularly in the less salt tolerant and faster-growing species (*R. apiculata*). Enhanced growth under elevated CO_2 was attributed to increased net assimilation rate as well as to increased leaf area ratio (under lower humidity) and improved PWUE. Farnsworth et al. (1996) also found that net photosynthesis of *R. mangle* grown at ambient CO_2 increased 22% when transferred to higher CO_2, and measured values were significantly higher than rates in plants grown and measured at elevated CO_2 concentrations.

More recently, the CO_2 response of black mangrove (*A. germinans*) growing alone and in mixture with a C_4 grass (*Spartina alterniflora*) has been investigated in an 18-month greenhouse study (McKee, 2006). This experiment used native sods of marsh in mesocosms (19 L containers) maintained at two nitrogen levels, targeting streamside and inland porewater concentrations of NH_4-N (0.5 and 10 $mol\,m^{-3}$) and two atmospheric CO_2 concentrations (365 and 720 $\mu l\,L^{-1}$) in replicate greenhouses. *A. germinans* responded to CO_2 enrichment with increased growth and biomass when grown alone, especially at higher nitrogen. However, seedling growth was severely suppressed when grown in mixture with *S. alterniflora*, and CO_2 and nitrogen enrichment could not reverse this effect.

4.3. Synthesis of CO_2 studies

Some important points can be made regarding potential effects of CO_2 on mangrove seedlings. First, the majority of experiments with other plant species indicate a huge range of potential growth enhancement for plants (Saxe et al., 1998). Given the taxonomic diversity of mangroves, there will likely be variable response to increases in atmospheric CO_2 due to inherent characteristics. The four species examined so far show a growth response to instantaneous and long-term exposure to elevated CO_2 ranging from −27 to 71% of ambient controls (Table 1). Second, elevated CO_2 can stimulate early growth of mangroves when grown in isolation under relatively optimal conditions. However, competition from other species may limit or prevent mangrove seedling response to CO_2 (McKee, 2006). This observation is consistent with other work showing that CO_2 response of plants grown in isolation is not predictive of future changes in vegetation (Poorter and Navas, 2003). Third,

Table 1
Summary of mangrove growth responses to elevated CO$_2$; responses (biomass, net primary productivity (NPP[a]) or relative growth rate (RGR)) given as a percent of controls grown under ambient CO$_2$

Species[b]	CO$_2$ Treatment		Other factors	Response		Citation
	Level	Duration		Type	% Change from control	
RHMA	700	408 Days	–	Biomass	+40	Farnsworth et al. (1996)
RHMA	700	408 Days	–	RGR	+21	Farnsworth et al. (1996)
RHMA	361–485	Instantaneous[c]	–	NPP	−14	Snedaker and Araujo (1998)
RHAP	700	14 Weeks	High humidity	RGR	+36	Ball et al. (1997)
RHAP	700	14 Weeks	Low humidity	RGR	+71	Ball et al. (1997)
RHST	700	14 Weeks	High humidity	RGR	+40	Ball et al. (1997)
RHST	700	14 Weeks	Low humidity	RGR	+25	Ball et al. (1997)
AVGE	720	18 Months	Low nitrogen	Biomass	+18	McKee (2006)
AVGE	720	18 Months	High nitrogen	Biomass	+35	McKee (2006)
AVGE	361–485	Instantaneous[c]	–	NPP	−12	Snedaker and Araujo (1998)
LARA	361–485	Instantaneous[c]	–	NPP	−27	Snedaker and Araujo (1998)
COER	361–485	Instantaneous[c]	–	NPP	−8	Snedaker and Araujo (1998)

[a] NPP, g CO$_2$ m^{-2} min^{-1}.

[b] AVGE, *Avicennia germinans*; COER, *Conocarpus erectus*; LARA, *Laguncularia racemosa*; RHAP, *Rhizophora apiculata*; RHMA, *Rhizophora mangle*; RHST, *Rhizophora stylosa*.

[c] Plant leaves were exposed to higher CO$_2$ concentrations only during the measurement (10–30 s).

mangrove response to elevated CO$_2$ during early growth may be delayed due to the presence of maternal reserves or other phenological factors (Farnsworth et al., 1996). Experiments must be of a sufficient duration (e.g., >1 year) to assess the potential to respond to CO$_2$. Fourth, the CO$_2$ response will generally depend on other growth-limiting factors such as salinity and nutrient availability. Thus far, it appears that mangroves growing under conditions of lower salinity and higher nutrient availability will show the greatest response to rising CO$_2$. Such settings occur at the transition between mangrove and other lowland tropical vegetation (Clark and Guppy, 1988; Lovelock et al., 2005); areas influenced by groundwater (Semeniuk, 1983; Mazda et al., 1990; Ovalle et al., 1990; Whelan et al., 2005) or high rainfall (Ewel et al., 1998b); and areas impacted by nutrient loading due to agricultural or urban activities (Valiela et al., 2001). Fifth, predictions that stress tolerance or competitive ability will be enhanced under elevated CO$_2$ are not supported by the work conducted thus far. Finally, CO$_2$-induced changes in tissue chemistry have been observed and may have consequences for susceptibility to photoinhibition (protective secondary compounds) or to herbivory (tissue palatability).

5. Salinity

Salinity is one of the most important drivers in mangrove establishment and early development (e.g., Ball, 2002). Most mangroves are facultative halophytes (i.e., they grow better in some salt but do not necessarily require it for growth), and studies have demonstrated that optimal growth rates occur in 5–75% seawater concentrations (Burchett et al., 1984, 1989; Naidoo, 1987; Hutchings and Saenger, 1987; Ball, 1988a; Smith and Snedaker, 1995), depending on species and seedling growth stage. Mangroves can grow in a range of salinities, extending from primarily freshwater environments into hypersaline areas (Chapman, 1976). All mangrove forests are exposed to some salinity, be it at daily, monthly, seasonal, or extreme tidal events (Watson, 1928). Accordingly, propagules have to be tolerant of a wide range of environmental conditions as most mangroves are passively dispersed via tides (Rabinowitz, 1978a,b; Hogarth, 1999). Inherent physiological and ecological tolerances influence not only plant physiognomy, but also interspecific and intraspecific competitive abilities.

5.1. *Specific salinity effects and coping mechanisms*

The ocean is approximately 35 parts per thousand (ppt) salt, depending on the degree of tidal exchange, freshwater input, and evaporation. This salt is 86% NaCl (483 mM Na$^+$, 558 mM Cl^{-1}). Mangroves, therefore, have to maintain continuous water uptake, and regulate ion uptake and compartmentation against a strong external salt gradient (Ball, 1996). To maintain water uptake, mangroves not only have to restrict water loss by having conservative morphological and physiological adaptations, but also they need to maintain sufficiently low water potentials. Agricultural crops under well-saturated conditions generally have water potentials of approximately -1.0 MPa. However, as the osmotic potential of seawater is approximately -2.5 MPa (Sperry et al., 1988), mangrove leaf water potentials have to range between -2.5 and -6.0 MPa (e.g., Scholander et al., 1966; Medina et al., 1995; Aziz and Khan, 2001; Sobrado and Ewe, 2006).

Maintaining low water potentials is achieved by passively accumulating and synthesizing both organic and inorganic molecules for osmotic adjustment. Mangroves accumulate inorganic ions such as sodium (Na$^+$) and potassium (K$^+$) (e.g., Sobrado, 2005; Naidoo, 2006; Sobrado and Ewe, 2006) as well as organic compounds (proline, glycinebetaine, mannitols, cyclitols, quartenary ammonium compounds) for osmotic regulation (Popp et al., 1984; Popp and Polania, 1989; Popp, 1995). Ions are accumulated in the vacuole while in non-vacuolar regions (i.e., cytoplasm, intercellular spaces), organic compounds are used in regulating salinity because mangrove enzymes and metabolic processes are just as sensitive to salts as those in non-halophytes (e.g., Flowers et al., 1977; Ball and Anderson, 1986; Larcher, 2001; Lüttge, 1997). Various researchers (e.g., Medina and Francisco, 1997; Paliyavuth et al., 2004; Sobrado, 2005; Sobrado and Ewe, 2006) have demonstrated that leaf and xylem sap osmolality increase with higher soil salinity.

In addition to accumulating osmotica, mangroves also exclude and secrete salts, and increase succulence as a means of maintaining ionic balance within the plant (Popp, 1995). Mangroves exclude uptake of at least 90% of the external salt (Scholander et al., 1962, 1966) in a physical process (Scholander, 1968; Werner and Stelzer, 1990) that occurs via the symplastic pathway at the tips of 3–4th order roots (Moon et al., 1986); this can lead to the salinization of the soil around the roots (Passioura et al., 1992). Consequently, mangrove water uptake rates and concurrent salt exclusion at the roots have to be balanced by the flushing rates of the surrounding soil by tides and rainfall.

All mangrove species have a range of salt-coping mechanisms. Some mangrove genera have salt excretion glands (e.g., *Avicennia* spp., *Sonneratia* spp., *L. racemosa*) while others accommodate salt in the shoots by increasing succulence (e.g., *Ceriops tagal, Xylocarpus* spp., *Osbornia* spp.) (e.g., Smith et al., 1989; Hogarth, 1999; Sobrado and Greaves, 2000; Suarez and Sobrado, 2000; Aziz and Khan, 2001). Salt excretion is an energy-dependent process that moves ions against large electrochemical potentials within the leaves (Lüttge, 1997). Consequently, salt-excreting mangroves have higher metabolic and nutritional demands than non-salt-excreting species, a tradeoff against higher growth rates at lower salinity conditions (Ball, 1996). In addition, salts are also translocated among the leaves to allow excess ion removal with leaf senescence (Cram et al., 2002). For example, K^+ is retranslocated from older leaves to younger leaves, resulting in increasing Na^+/K^+ ratios in senescing leaves (Werner and Stelzer, 1990; Cram et al., 2002; Wang et al., 2003).

5.2. *Influence of salinity on propagule establishment*

Ungar (1982) observed that the early seedling stage was likely the most sensitive life stage in halophytes. In a laboratory study, McMillan (1971) observed that *A. germinans* propagules were able to produce roots in salt contents ranging from 0 to 57 ppt but only 10% of propagules in 75 ppt were able to root. Leaf emergence rates for two subspecies of *Ceriop tagal* decreased with increasing salinity and mortality was greatest at 60 ppt (Smith, 1988). At salinity >25 ppt, seeds of *Acanthus ilicifolius* failed to germinate (Ye et al., 2005).

Propagules prematurely abscised from the parent plant and newly emergent seedlings are prone to desiccation if they fail to strand or root properly (Ewe, unpublished data). Although most mangrove propagules can tolerate a wide range of salinities, the persistence and exposure to physical and physiological desiccation increases with temperature and increased salinity.

5.3. *Influence of salinity on propagule/seedling development*

The optimal range of physiological function and growth of seedlings is approximately from 3 to 27 ppt (e.g., Field, 1984; Hutchings and Saenger, 1987; Ball and Pidsley, 1995; Aziz and Khan, 2001) although salinity optima have been shown to vary with seedling age (Hutchings and Saenger, 1987). Above or below the optimal salinity, gas exchange and growth are reduced (e.g., Ball and Farquhar, 1984; Ball, 1988a; Ball et al., 1997; Tuffers et al., 2001; Munns, 2002; Krauss and Allen, 2003a; Biber, 2006).

Photosynthesis of mangroves, like that of many vascular woody plants, on average ranges between 5 and 20 μmol CO_2 m^{-2} s^{-1} (e.g., von Caemmerer and Farquhar, 1981; Andrews et al., 1984; Clough and Sim, 1989; Naidoo et al., 2002). Under favorable conditions of low salinity, the rate of photosynthesis can exceed 25 μmol CO_2 m^{-2} s^{-1} (Clough and Sim, 1989). At higher salinities, gas exchange becomes restricted by both stomatal and non-stomatal (i.e., biochemical) limitations in many halophytes (e.g., Flowers and Yeo, 1986; Kozlowski, 1997; Munns, 2002).

When freshwater is limiting (i.e., physiological drought) mangroves have to be more restrictive with water loss. Stomatal restrictions reduce photosynthesis and transpiration rates and increase PWUE (Ball and Farquhar, 1984; Clough and Sim, 1989; Lin and Sternberg, 1992; Sobrado and Ball, 1999; Sobrado, 2005). Mangroves exhibit conservative water use patterns relative to other woody vascular plants as increased water use efficiency is an effective mechanism at maintaining metabolic function in highly saline environments (Clough, 1992; Sobrado, 2000, 2001). Transpiration is decoupled from salt exclusion at the roots, since salt flux to the leaves does not increase with higher transpiration (Ball, 1988a). Instead, stomatal constraints restrict water loss under conditions of limited water availability. In what is known as the dessication–starvation dilemma (Lüttge, 1997), plant CO_2 uptake for growth occurs simultaneously with transpirational water loss via the stomates. Consequently, to grow, mangroves have to allow for some degree of water loss. The observed patterns of growth in mangroves may have developed as strategies to avoid vascular embolisms and excess salt accumulation around the roots (Ball and Passioura, 1994).

At high salinities, the non-stomatal limitations to gas exchange are purportedly the result of biochemical damage to a leaf's Photosystem II: chronic exposure to salinity can lead to the collapse of plant biochemical function, cell damage, and ultimately plant death (Flowers and Yeo, 1986). However, studies of *Avicennia marina* and *A. germinans* have not demonstrated these biochemical impairments. Instead, reduced net carbon assimilation at 60 ppt was a function of higher PWUE coupled with greater photorespiration (Sobrado and Ball, 1999); similar observation was also found in *R. mangle* by López-Hoffman et al. (2006).

Growth responses of congeneric (e.g., Ball and Pidsley, 1995) and sympatric (e.g., Cardona-Olarte et al., 2006) mangrove seedlings have been shown to differ across a range of salinities and with salinity fluxes. Increasing salt tolerance, however, is at the expense of higher nutritional demands and lower maximal growth rates at low salinities (Ball, 1988a, 1996). Exposure to a constant salinity level might even be less physiologically demanding on a seedling than fluctuating salinity levels. For example, Lin and Sternberg (1992) showed that growth and leaf gas exchange rates of *R. mangle* were lower under fluctuating salinities compared to constant salinities. Prolonged high salinity exposure may result in restricted growth due to water uptake limitations: leaves become small and thick (e.g., Camilleri and Ribi, 1983; Medina and Francisco, 1997; Sobrado, 2001) and plants have less leaf area than those growing at lower salinity (Naidoo, 2006).

6. Light

Salinity limits water uptake in mangroves (Scholander, 1968; Clough, 1984) and causes decreased photosynthetic rates (Ball and Farquhar, 1984; Ball et al., 1987; Clough and Sim, 1989; Sobrado, 1999), but it is also important to note that conservative water use and low photosynthetic rates have consequences for mangrove light relations. First, the mangrove environment predisposes mangroves to the potential for photoinhibition (Björkman et al., 1988). Second, there are interactive effects between salinity and light; the mangrove light response depends on the salinity level of the growth environment (Ball, 2002; Krauss and Allen, 2003a; López-Hoffman et al., 2007a).

6.1. Photoinhibition

The saline environment and the potential for high radiation levels in tropical latitudes make avoiding photoinhibition a particular challenge for mangroves (Björkman et al., 1988). Accordingly, mangroves almost universally experience low stomatal conductances, high PWUE, and low light-saturated rates of photosynthesis (Farquhar et al., 1982; Ball and Farquhar, 1984; Krauss et al., 2006a). These strategies necessitate that mangroves protect proteins associated with photochemistry (especially Photosystem II, Osmond, 1994), as energy associated with the narrowest wavelengths of light are absorbed in excess by chlorophyll. Photoinhibition occurs when low photosynthetic rates combined with high radiation loads lead to an excess of excitation energy – more light is absorbed than can be used in photosynthesis. Typically, mangrove photosynthetic rates saturate at 40% irradiance or less (Ball and Critchley, 1982; Cheeseman, 1991), suggesting that irradiance may often be excessive.

However, mangroves have an uncanny capacity for avoiding photoinhibition (Cheeseman, 1991; Fig. 4). Yet, mangroves fluoresce light commensurate with higher rates of O_2 evolution from photosynthesis. Mechanistically, aside from some pre-filtering of ultraviolet radiation with phenolic compounds (Lovelock et al., 1992), photosystem quenching of absorbed light might be attained at least in part by absorbing photochemically derived electrons with excessive oxygen production from the physical processes of light capture (Cheeseman et al., 1997). Mangroves can also alter rate constants affecting the capacity for heat dissipation between photosystems through antenna complexes (Björkman et al., 1988). Important recent studies suggest that the combination of mechanisms used to avoid photoinhibition differs between species (Christian, 2005). For example, Lovelock and Clough (1992) determined that *Rhizophora* spp. rely more on vertical leaf-angles, while *Bruguiera* spp., which have horizontonally displayed leaves, are protected by larger xanthophyll pigment pools.

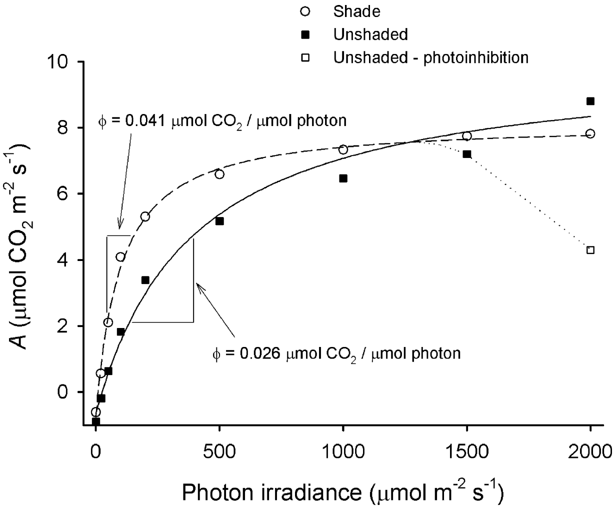

Fig. 4. Photosynthetic assimilation (A) of *Rhizophora mangle* leaves grown while shaded (○) versus unshaded (■) in a greenhouse in Hawaii. Quantum yield (ϕ) was higher in shade-grown leaves indicating a greater efficiency of energy conversion relative to unshaded leaves (as per Björkman et al., 1988). Shaded seedlings did not differ from unshaded seedlings in overall photosynthetic potential (Krauss and Allen, 2003a). Mangroves are unique in that they do not readily exhibit photoinhibition, as might occur according to the hypothetical curve drawn here (□).

Because stomatal conductance and photosynthetic rates decrease with an increase in salinity, it might be expected that photoprotective responses should increase with salinity. Indeed, in an early laboratory study, Björkman et al. (1988) observed an increase in photoprotection in *R. stylosa* and *A. marina* with an increase in salinity from 10 to 100% seawater. However, a more recent field study with *A. marina* revealed no differences in photoprotection between 100 and 200% seawater treatments, possibly due to photorespiratory electron consumption (Sobrado and Ball, 1999). Further research is needed to understand photoinhibition and photoprotection in response to increased salinity (see also Christian, 2005), and changes in atmospheric CO_2 (see Section 4, above).

6.2. Interactive effects of light and salinity

In mangroves, conservative leaf-level water use and low photosynthetic rates result in reduced carbon gain at high salinity (Ball, 1988b). This pattern suggests that the negative effects of salinity on leaf-level carbon gain should be greater at higher light levels, because at high light, photosynthesis is limited by conductance (Lambers et al., 1998). Several recent studies have shown that the combination of high light and high salinity may be most limiting to mangrove carbon gain and growth (Ball, 2002; Krauss and Allen, 2003a; López-Hoffman et al., 2007a).

In greenhouse experiments, seedling carbon gain increased more with an increase in light at low salinity than at high salinity, 20 and 167% seawater, respectively (López-Hoffman et al., 2006, 2007a). At high salinity relative to low salinity, stomatal conductance, leaf transpiration, and internal CO_2 concentrations were lower, and the ratio of leaf respiration to assimilation was much greater. Thus, stomatal limitations and increased respiratory costs may explain why at high salinity, seedlings are unable to respond to increased light levels with increased carbon gain (López-Hoffman et al., 2007a).

Consistent with the leaf-level, at the whole plant level, mangrove seedling mass and growth rate increase more with an increase in irradiance at low than high salinity (Ball, 2002). In addition, interactive effects of salinity and light have been observed in seedling biomass allocation patterns (López-Hoffman et al., 2007a). Mangrove seedlings at low salinity exhibit the typical plant response to increased irradiance: increased root mass and decreased leaf mass (Bouwer, 1962). However, at high salinity when seedlings already have a high root mass and root/leaf ratio, they did not further allocate to roots in response to increased light (López-Hoffman et al., 2007a).

Species differences in mangrove responses to the interactive effects of light and salinity may explain important differences in forest structure. In a study of Hawaiian mangroves, it was determined that the highly invasive, *R. mangle*, performs better under high light, high salinity conditions than the less invasive *Bruguiera sexangula*. This may explain why in moderate and high salinity zones, *R. mangle* is the canopy dominant and *B. sexangula* occurs only in the understory (Krauss and Allen, 2003a).

6.3. *Interactive effects of light and nutrients*

At lower nutrient and light levels, mangrove seedlings invest more in allocation to roots than to leaves. At higher nutrient levels, more biomass is allocated to leaves (McKee, 1995). As light increases, increased root mass at the expense of leaves is associated with greater requirements for water and nutrients (van den Boogaard et al., 1996). Furthermore, species differences to light and nutrients were more pronounced at high nutrient and light combinations (McKee, 1995).

6.4. *The importance of light gap dynamics*

The importance of canopy gaps for mangrove forest dynamics and regeneration have been investigated (Smith et al., 1994; Ewel et al., 1998c; Feller and McKee, 1999; Sherman et al., 2000; Duke, 2001; Clarke, 2004). Numerous studies have examined the effects of canopy gaps on mangrove seedling establishment and growth (Putz and Chan, 1986; Smith, 1987c; Ellison and Farnsworth, 1993; McKee, 1995; McGuinness, 1997; Osunkoya and Creese, 1997; Sousa et al., 2003a). Some studies report higher seedling establishment and growth in gaps (e.g., Putz and Chan, 1986). Others report similar seedling establishment and survival rates in gaps and non-gaps, but higher seedling growth rates, and higher sapling densities in gaps (e.g., Clarke and Allaway, 1993; Clarke and Kerrigan, 2000). All of these studies discuss seedling light response and conclude that light gaps are important for mangrove forest dynamics. However, successful seedling colonization and initial growth may be followed by differential survivorship and progression to the juvenile stage within light gaps (López-Hoffman et al., 2007b).

Several studies have attempted to address the influence of canopy gaps by assessing juvenile densities as well as seedling growth (Clarke and Allaway, 1993; Clarke and Kerrigan, 2000; Whelan, 2005). One outcome of this work is a reconsideration of the gap dependence of *R. mangle*, historically considered a shade-tolerant species (Ball, 1980). The observation that *R. mangle* seedlings can establish at all light levels and that juvenile density is higher in gaps (Smith et al., 1994; Sousa et al., 2003b; Whelan, 2005), suggests that *R. mangle* may be dependent on gaps for regeneration (Whelan, 2005). This observation is supported by individual-based model simulations of mangrove population dynamics which indicate that *R. mangle* is dependent on light gap disturbances (Chen and Twilley, 1998; Berger and Hildenbrandt, 2000; Berger et al., 2006, 2008; López-Hoffman et al., 2007b).

More demographic studies are needed on the role of gaps in mangrove life histories and population dynamics. Furthermore, given the interactive effects of salinity and light on mangrove seedling performance (Ball, 2002; Krauss and Allen, 2003a; López-Hoffman et al., 2007a) and the influence that gaps have on soil characteristics (Ewel et al., 1998c), it will be important to compare the role of light gaps in low and high salinity mangrove forests.

7. Nutrients

In almost all plant communities nutrient availability is an important driving variable influencing community structure (Grime, 1979; Chapin, 1980; Tilman, 1987). This is also the case for mangrove forests (e.g., Onuf et al., 1977; Boto and Wellington, 1983; Lovelock and Feller, 2003). Mangroves occupy soils with a wide range of nutrient availability. Many mangrove environments have extremely low nutrient availability due to infertility of upland soils in tropical regions and limited terrigenous input (e.g., Lovelock et al., 2005). For example, on oceanic islands in the Caribbean where the peat soil substrate is comprised of mangrove roots, newly initiated roots colonize earlier root channels, mining for extremely low levels of nutrients (McKee, 2001).

Most mangrove species that have been studied have been found to be highly sensitive to variation in nutrient availability both in the laboratory (e.g., Boto et al., 1985; Naidoo, 1987; McKee, 1996; Yates et al., 2002) and in the field (e.g., Boto and Wellington, 1983; Feller, 1995; Koch, 1997; Feller et al., 2003, 2007; Lovelock et al., 2005, 2007; Naidoo, 2006). In the Atlantic East Pacific biogeographic province the response of the three dominant species, *R. mangle*, *A. germinans* and *L. racemosa*, to nutrient availability has been considered in multiple studies, but in the Indo-West Pacific region few studies documenting the effects of nutrient availability on mangrove species performances have been published. This is a large knowledge gap, given most of the mangrove forests of the world are within this latter region, and that they are under intense pressure from development but are extremely important for the sustainability of coastlines and coastal populations (Valiela et al., 2001; Alongi, 2002; Dahdouh-Guebas et al., 2005; Walters et al., 2008).

Enhancements in nutrient availability have mostly led to faster growth rates which are associated with an increase in allocation to leaf area relative to roots, along with a suite of physiological changes that include increased hydraulic conductivity and photosynthetic rates, and decreased efficiencies in nutrient resorption and use (McKee, 1996; Lovelock et al., 2004, 2006a). The responses to enhancements in the level of limiting nutrients are similar in mangroves as those observed in other species (Chapin, 1980). However, in some settings where high salinity, extreme aridity, or shade limits growth, nutrient additions have not enhanced growth (McKee, 1995; Lovelock and Ewe, unpublished data). Responses to nutrient additions are thus dependent on environmental conditions and on the identity of the species. Below we outline the traits that favor persistence of seedlings at low and high nutrient availability, and we consider the tradeoffs among traits that become important as other environmental parameters vary.

Species differences in both tolerance of low nutrient environments, and competitive ability under high levels of nutrient availability are often reflected in field distribution. For example, *R. mangle* often dominates in low nutrient environments, while *A. germinans* is often dominant in areas with higher nutrient availability (Sherman et al., 1998; McKee, 1993). What are the key physiological traits for seedlings of species that lead to tolerance of low nutrient environments and conversely foster a competitive nature under high nutrient availability?

7.1. Seedling traits beneficial in low nutrient environments

7.1.1. High biomass allocation to roots relative to shoots

Enhanced allocation to root biomass relative to shoot biomass is a common adaptation to low nutrient availability. In particular, allocation to fine versus coarse root biomass can greatly increase the surface area for nutrient absorption, especially in microsites of higher nutrient availability (Blair and Perfecto, 2001; Hodge, 2004). Fine root biomass, as a proportion of total biomass is usually higher in *R. mangle* compared to *A. germinans* (McKee, 1995). Additionally fine roots of *R. mangle* decompose slowly compared to those of *A. germinans* thereby slowing nutrient release and loss (Middleton and McKee, 2001). In more diverse forests of Asia, Komiyama et al. (2000) found that variation in shoot/root ratios was large and varied among species (Table 2). A general pattern of higher allocation to roots compared to shoots in representatives of the Rhizophoraceae, indicate that species of this family are more tolerant of low nutrient conditions than those of other families.

Table 2
Variation in shoot to root ratio in forests dominated by different mangrove genera

Mangrove genera	Shoot/root ratio
Sonneratia	5.25
Bruguiera	3.01–4.58
Rhizophora	1.71–2.66
Ceriops	1.05
Temperate forest	2.7–3.7
Tropical forest	5.1–10.7

Ratios for terrestrial, temperate, and tropical forests are given for comparison (from Komiyama et al., 2000)

7.1.2. High levels of maternal reserves

Many mangrove species have large propagules (Tomlinson, 1986). The reserves contained within them support growth for an extended period of time. Ball (2002) observed that for seven species of the Rhizophoraceae, those with the largest propagule mass were larger after 1 year of growth compared to those species with smaller mass, although propagule mass did not influence survival. Similar importance of propagule size on intraspecific seedling vigor was reported for *R. mangle* (Lin and Sternberg, 1995). The nutrient status of the maternal tree and the provisioning of propagules may thus have a large influence on early seedling growth.

7.1.3. High levels of nutrient resorption

Prior to tissue senescence a proportion of the nutrient capital invested in the tissue is resorbed in the phloem to be allocated to new tissue. Nutrient resorption can be highly efficient in *R. mangle*, reaching maximum values recorded for angiosperms of 85% of phosphorus resorbed prior to senescence of leaves (Feller, 1995). In tidal environments where surface litter may be washed away, the evolution of high resorption efficiency may be particularly important to tolerating low nutrient concentrations, particularly in seedlings. Resorption efficiency declines with increases in the level of available nutrients (Feller, 1995; Feller et al., 2002; McKee et al., 2002). Resorption efficiency varies among mangrove species and is generally lower in *A. germinans* than in *R. mangle* under the same conditions (Feller et al., 2007). This trend is consistent with other traits of these two species, where *A. germinans* has higher maximum growth rates and higher nutrient concentrations in leaf tissue compared to the more conservative *R. mangle*.

7.1.4. High nutrient use efficiency of photosynthesis and other processes

In mangroves, photosynthetic nutrient use efficiency (i.e., maximum photosynthetic rate per foliar nutrient content: Field and Mooney, 1986) is high under limiting nutrients and declines with increasing nutrient availability (e.g., Feller et al., 2003). At low nutrient availability, species differ in their nutrient use efficiency. The limited data suggest *Rhizophora* has higher nutrient use efficiency than *Avicennia*, although this order can be altered under differing salinity regimes (Lin and Sternberg, 1992). Root respiration, per unit biomass, and thus possibly per unit nutrient absorbed, is also very low in mangroves (McKee, 1996) and particularly so in *R. mangle* (McKee, 1996; Lovelock et al., 2006b). The capacity of mangroves to tolerate and to utilize high levels of ammonium may also be an important process that reduces the cost of nitrogen uptake by reducing the activity of nitrate reductase (Turnbull et al., 1996; Britto et al., 2001).

7.1.5. Schlerophylly and tissue quality

Schlerophylly, which varies in leaves among species (e.g., Ball, 1988b), has been suggested to be an important trait for nutrient conservation. Tough, thick, carbon-rich leaves, and presumably tough roots reduce herbivory and slow decomposition, leading to retention of nutrients within plants and soils (e.g., Feller, 1995; Middleton and McKee, 2001). Typically leaves and roots of species within the Rhizophoraceae have higher levels of schlerophylly and higher C:N ratios than those of the Avicenneaceae, Combretaceae, and other families (Table 3; Rao et al., 1994; McKee, 1995).

7.1.6. Mutualisms and other strategies for increasing nutrient availability

Mangroves have been observed to have vesicular arbuscular mycorrhizal (VAM) associations at low salinity (<25 ppt: Sengupta and Chaudhuri, 2002), but growth benefits of these associations have yet to be determined. Highly anaerobic soils may also prevent exploration of the soil by symbiotic VAM fungi (Kothamasi et al., 2006). Mangrove roots are also associated with N-fixing microorganisms, which may enhance soil nutrient availability (Bashan and Holguin, 2002; Kothamasi et al., 2006). The exudation of extracellular enzymes by either plants or soil bacteria may also increase nutrient availability (Rojas et al., 2001) and facilitate nutrient acquisition in low nutrient environments. Other work using stable isotopic analyses suggests a facultative mutualism between *R. mangle* and encrusting epibionts growing on prop roots (Ellison et al., 1996). Values of δ^{15}N and δ^{13}C indicate that *R. mangle* growing along tidal creeks obtains inorganic nitrogen from sponges encrusting the prop roots submerged in tidal creeks and sponges obtain carbon from root exudates (Ellison et al., 1996). It is not known to what degree seedlings use similar strategies.

Table 3
C:N ratio of mangrove species from Gazi Bay (data from Rao et al., 1994)

Mangrove genera	C:N ratio
Rhizophora	78 ± 9
Bruguiera	70 ± 9
Ceriops	69 ± 4
Xylocarpus	39 ± 7
Lumnitzera	39 ± 1
Sonneratia	34 ± 1
Avicennia	27 ± 5
Heritiera	24 ± 1

7.2. Seedling traits beneficial in high nutrient environments

7.2.1. Large allocation to leaf area, high net assimilation rates, and rapid growth

Under high nutrient availability, traits that confer enhanced growth rates and facilitate occupation of space, shading of competitors, and monopolization of nutrient resources lead to canopy dominance (Poorter and Nagel, 2000). High growth rates are correlated with a suite of traits including reduced investment in carbon based defenses and structural tissues. Leaves are thinner, tannin concentrations are lower, and wood is less dense in fast growing compared to slow growing seedlings (Chapin, 1991; McKee, 1995).

7.2.2. High PWUE

Under saline conditions, high growth rates are associated with high levels of water use during photosynthesis, which due to extraction of water for transpiration, salinizes the soil (Passioura et al., 1992). Salinization reduces the likelihood of the establishment of less salt tolerant competitors. Species of *Avicennia*, with their fast growth rates and capacity to withstand high salinity soils, may exclude other competitors in this way (Lovelock and Feller, 2003). Removal of the influence of adult roots enhanced growth of seedlings (Ball, 2002), which may reflect intense below ground competition or interference competition by salinization of soils. These are important traits for sustained dominance in the upper intertidal zone.

7.3. Tradeoffs and interactions with other factors

Many traits that lead to fast growth under high levels of nutrient availability are not favorable under conditions of environmental stress (Field et al., 1983; Chapin, 1991). Moreover, species differ in their capacity to withstand abiotic stress, and these differences lead to the complex situation where a species' capacity to acquire nutrients is moderated by the interaction between its inherent stress tolerance and the environmental setting in which it grows. For example, at a hypersaline site in Florida, growth of *A. germinans,* which is tolerant of high soil salinity, benefited from fertilizer additions, while *L. racemosa* showed lower growth enhancement with fertilization (Lovelock and Feller, 2003). At the leaf level, *L. racemosa* growth responses to fertilization were limited because this species had lower PWUE under saline field conditions than *A. germinans*. Low PWUE of *Laguncularia* gives rise to sensitivity to increasing salinity, where photosynthetic rates decline when salinity is high, resulting in reduced ability to utilize available nutrients. The differences in water and nutrient use efficiency among species may thus facilitate coexistence of *Laguncularia* and *Avicennia* under moderate salinity levels and low nutrient availability, while dominance of *Avicennia* would be predicted with hypersalinity and high nutrient levels, and dominance of *Laguncularia* predicted with low to moderate salinity and low nutrient availability.

Allocation of biomass to roots relative to shoots (Table 2) reduces growth rates and increases the potential for nutrient acquisition. A significant proportion of fixed carbon in mangrove seedlings is lost through root respiration (PRR), and differences among *R. mangle* (20%), *A. germinans* (12%), and *L. racemosa* (8%) are inversely correlated with these species potential growth rates (McKee, 1995, 1996). Since the PRR partly reflects the proportion of biomass allocated to roots, an increase in root biomass to acquire limiting nutrients will also increase carbon loss to respiration and, consequently, overall growth. In addition to belowground roots, allocation of carbon to aboveground roots increases tolerance of anoxic soil conditions (McKee et al., 1988; McKee, 1996; Cardona-Olarte et al., 2006). Seedlings of species that can allocate high levels of carbon to aboveground roots (species within the family Rhizophoraceae) and also those that can modify their wood and bark anatomy (Yáñez-Espinosa et al., 2001), trade high growth rates for a strategy that ensures tolerance of, and dominance in, nutrient poor, low intertidal, and permanently flooded habitats (Cardona-Olarte et al., 2006).

8. Flooding and sea-level rise

8.1. Experimental studies on flooding

Flooding of mangrove communities can range naturally from seasonally tidal to near-permanent (Watson, 1928). Some mangroves respond to flooding by altering internal biochemical processes or by producing lenticels on basal stems or root structures to help offset the effects of lower soil oxygen levels (Tomlinson, 1986). During a flood event, oxygen concentrations in the soil can be reduced rapidly by as much as 28% after 6 h of flooding and as much as 72% after 20 h under experimental culture (Skelton and Allaway, 1996). Flooding alters soil condition so much that mangrove seedlings can respond as much to by-products imposed by flooding as to surface water alone (McKee, 1993; Youssef and Saenger, 1998). Lower oxygen partial pressures are reflected in root aerenchyma shortly after the onset of flooding (0.5–24 h) (McKee, 1996). Under flooding or experimental hypoxia, mangrove roots may metabolize anaerobically for short periods of time, allowing some energy production to continue (McKee and Mendelssohn, 1987; Chen et al., 2005). However, the most effective strategy is to avoid root hypoxia through internal aeration.

Differing soil oxygen states have been induced experimentally (Pezeshki et al., 1989). Anoxia alone can reduce photosynthesis by 39% for some mangrove seedlings relative to oxygen-rich controls (Pezeshki et al., 1997). However, stomatal conductance remained unaffected even though concentrations of root alcohol dehydrogenase (ADH) increased as soil oxygen concentrations decreased (Pezeshki et al., 1997). ADH, which is typically produced in roots as a catalyst to fermentation in response to flooding, can be stimulated in some species by lower root oxygen tensions (McKee and Mendelssohn, 1987), but the effects of ADH can be quite variable on leaf gas exchange in mangroves. For example, an increase in ADH activity in roots of *Kandelia candel* seedlings corresponded to reduced photosynthesis with prolonged flooding (Chen et al., 2005).

Leaf transpiration, photosynthesis, and growth of seedlings remained unaffected by experimentally induced hypoxia over 12 weeks; however, species differed in their abilities to maintain root aeration under these conditions (McKee, 1996). Current research suggests that mangrove seedlings can avoid flooding stress by maintaining high root oxygen concentrations (McKee, 1996) or by aerating the immediate rhizosphere (Thibodeau and Nickerson, 1986; McKee et al., 1988), which creates a buffer zone for oxidation of potentially toxic sulfide (McKee, 1993). The oxidized rhizosphere also may act as a boundary layer, minimizing the flux of oxygen from roots to the bulk soil, thereby conserving oxygen within the root system. The capacity for these two strategies may be juxtaposed in mangrove seedlings, since the ability to conserve oxygen promotes less oxygen diffusion to the soil adjacent to the roots (Youssef and Saenger, 1996).

There are a few studies that have established appropriate controls to address seedling responses to actual flood events (Table 4). In one of the earlier evaluations (Pezeshki et al., 1990), flooding of the soil surface with fresh water had no effect on leaf gas exchange or PWUE for three mangrove species over a 180-day period. Flooding did lead to a reduced leaf size in *L. racemosa* and *R. mangle*, and a reduced leaf dry weight in *A. germinans*. Flooding can create an overall reduced photosynthetic capacity and growth potential for seedlings by prompting a reallocation of leaf and whole-seedling biomass. This was evident for *R. mangle*, for example, where individual seedlings produced less total biomass while flooded (Pezeshki et al., 1990). Yet, evaluating flood effects alone in the absence of salinity is, in itself, problematic. Mangroves are facultative halophytes; maximum growth is realized under some optimal salinity concentration (see Section 5, above). In addition, flooding of seedlings by saltwater promotes a greater demand for osmotic adjustment than flooding by fresh water alone (Naidoo, 1985).

Field observations and experimental studies have established that many mangroves also grow best around optimum flood levels and durations (Fig. 1). Ellison and Farnsworth (1993), for example, found that growth and survival of *A. germinans* seedlings were compromised at intertidal positions indicative of either greater or lesser flooding from that of mean water level. *R. mangle* fared better at the deeper water levels and longer hydroperiods indicative of lower intertidal positions (Ellison and Farnsworth, 1993). Similarly, among neotropical mangroves *R. mangle* generally survives within the broadest range of flood durations (Koch, 1996; Cardona-Olarte et al., 2006; Krauss et al., 2006b). Other mangrove seedlings partition responses similarly. For example, the relative growth rates of *Bruguiera gymnorrhiza* decreased with duration of flooding, while *K. candel* experienced no such reductions by allocating less carbon belowground in response to flooding (Ye et al., 2003). Flooding also affected both stomatal conductance and leaf water potential for *B. gymnorrhiza* seedlings (Naidoo, 1983), while tidal flooding reduced seedling height, diameter, leaf area, leaf biomass, stem biomass, and root biomass for *B. gymnorrhiza* relative to saturated controls (Krauss and Allen, 2003b). Seedlings of *K. candel* had reduced photosynthetic

Table 4
Summary of experimental studies conducted on the effects of environmental drivers on mangrove establishment and development associated with flooding and sea-level rise

Species[a]	Geographic location of study system	Stressor	Variable[b]	Study type[c]	Growth form[d]	Experiment duration (days)	Source
AVGE, LARA, RHMA	Belize	Anoxia	g, p	G	sdl	84	McKee (1996)
AVGE, RHMA	Florida, USA	Anoxia	g, p	G	sdl	60	Pezeshki et al. (1997)
AECO, AVMA, BRGY, RHST	Australia	Anoxia	p	G	sdl	28	Youssef and Saenger (1998)
AVGE, RHMA	Belize	Flood depth	g	F	sdl	365	Ellison and Farnsworth (1993)
AVMA	Qatar	Flood depth	p	G	sdl	14	Sayed (1995)
AVOF, BRCY, CETA, RHAP, RHMU, SOAL, XYGR	Thailand	Flood depth	g	F	sdl	365	Kitaya et al. (2002)
BRGY	South Africa	Flood duration	p	G	sdl	80	Naidoo (1983)
AVMA, BRGY, RHMU	South Africa	Flood duration	g, p	G	sdl	60	Naidoo (1985)
RHMA	Florida, USA	Flood duration	g	F	tre	530	Lahmann (1988)
AVGE, LARA, RHMA	Florida, USA	Flood duration	g, m, p	G	sdl	180	Pezeshki et al. (1990)
BRGY, KACA	Hong Kong	Flood duration	g, p	G	sdl	84	Ye et al. (2003)
AVGE, LARA, RHMA	Florida, USA	Flood duration	g, m, p	G	sdl, sap	424	Krauss et al. (2006a,b)
LARA, RHMA	Florida, USA	Flood duration	g, m	G	sdl	276–367	Cardona-Olarte et al. (2006)
AVMA	South Africa	Short-term flood pulse	p	F	tre	5–10	Naidoo et al. (1997)
AVGE, LARA, RHMA	Florida, USA	Short-term flood pulse	p	G	sdl, sap	6–22	Krauss et al. (2006a)
AVGE, LARA, RHMA	Florida, USA	Short-term flood pulse	p	F	tre	1–2	Krauss et al. (2007)
KACA	China	Tidal flood duration	g, p	G	sdl	70	Chen et al. (2004, 2005)
BRGY	China	Tidal flood duration	m	G	sdl	70	Wang et al. (2007)
AECO, AVMA, BRGY, RHST	China	Tidal flooding	g	F	sdl	365	He et al. (2007)
BRGY	Micronesia	Tidal flooding	g	G, F	sdl	178, 349	Krauss and Allen (2003b)
XYGR	Micronesia	Tidal flooding	g	G	sdl	178	Allen et al. (2003)
LARA, RHMA	Florida, USA	Tidal flooding	g, m	G	sdl	276–367	Cardona-Olarte et al. (2006)
RHMA	Belize	Tidal sea-level rise	g, m, p	G	sdl, sap	823	Ellison and Farnsworth (1997)
BRGY, KACA	Hong Kong	Tidal sea-level rise	g, m, p	G	sdl	120	Ye et al. (2004)

[a] AECO, *Aegiceras corniculatum*; AVGE, *Avicennia germinans*; AVMA, *Avicennia marina*; AVOF, *Avicennia officinalis*; CETA, *Ceriops tagal*; BRCY, *Bruguiera cylindrica*; BRGY, *Bruguiera gymnorrhiza*; KACA, *Kandelia candel*; LARA, *Laguncularia racemosa*; RHAP, *Rhizophora apiculata*; RHMA, *Rhizophora mangle*; RHMU, *Rhizophora mucronata*; RHST, *Rhizophora stylosa*; SOAL, *Sonneratia alba*; XYGR, *Xylocarpus granatum*.

[b] Growth (g), morphological (m), physiological (p).

[c] Greenhouse (G), field (F).

[d] Seedling (sdl), sapling (sap), tree (tre).

light saturation levels and photosynthesis with longer immersion periods (Chen et al., 2005). Oddly, tidal flooding enhanced biomass attributes for *Xylocarpus granatum* seedlings, even though this species typically occurs naturally under low flood frequencies and durations (Allen et al., 2003). It is apparent that specific characteristics of flooding are important on a species-specific basis, but in general, seedling physiological efficiency and growth potential are reduced with increased flood durations and depths beyond some optimum.

Plant age might also be important for how mangroves respond to flooding. Leaves of young *A. marina* trees (1–2 m tall) had similar photosynthetic rates and greater stomatal conductance while flooded with dilute seawater than when unflooded on field sites (Naidoo et al., 1997), and saplings of *R. mangle* had higher photosynthesis and PWUE while flooded versus drained on some field sites in south Florida (Krauss et al., 2006a). This pattern suggests that mangroves may become less sensitive to flooding either with prolonged (and previous) exposure or with plant age. These hypotheses were tested experimentally by partitioning flood responses among seedling, sapling, and mature trees. First, seedlings (<1 m tall) and saplings (>1 m tall) were exposed to a range of flood durations experimentally over two growing seasons (Krauss et al., 2006a). No differences were registered among three neotropical mangrove species in dark respiration (R_d), quantum yield, photosynthesis, light compensation point, light level required to attain 1/2 of maximum photosynthesis (K), or PWUE for flood durations of 0, 189, or 424 days. However, short-term flooding of 6–22 days stimulated a 20% reduction in maximum photosynthesis, 51% lower K, and a 38% higher demand from R_d in both seedlings and saplings (Krauss et al., 2006a). Second, growth was generally maximized at moderate to permanent flood durations (Krauss et al., 2006b). Field studies, on the other hand, indicate that the interrelatedness of site hydroperiod and soil P concentrations control growth of mangroves more than hydroperiod alone under many conditions (Chen and Twilley, 1999; McKee et al., 2002; Krauss et al., 2006b). Third, short-term flooding did reduce sap flow in mature *R. mangle*, *A.*

germinans, and *L. racemosa* trees (Krauss et al., 2007) similarly to reductions registered for seedlings and saplings, and suggested that seedlings might actually provide a surrogate for rating environmental effects on mature trees. Overall, flooding appears to stall physiological processes associated with photosynthetic light initiation in seedlings and saplings, but recovery after prolonged exposure under some conditions is probable.

8.2. Sea-level rise

The overall persistence of mangrove ecosystems as global sea levels rise is ultimately controlled by shoreline geomorphology, sedimentation, and the actual rate of sea-level rise for a particular coastline (Woodroffe, 1990, 1999; Semeniuk, 1994; Gilman et al., 2008). Individual plant responses are also important, and have been the focus of a few recent experimental studies. One year old seedlings of *A. marina*, for example, were subjected to a prolonged high tide (14 days) associated with projected sea-level rise (Sayed, 1995). As expected, stomatal conductance declined rapidly (within 1 day) and leaf xylem water potentials also decreased. More importantly, the recovery of these functions was rapid once simulated high tides were removed.

In a 2½-year study, responses of tidally maintained *R. mangle* seedlings were compared under three relative tidal flood regimes simulating high (+16 cm), static, and low (−16 cm) sea levels (Ellison and Farnsworth, 1997). Seedlings maintained 1–7% fewer stomata per unit area, 6–21% greater photosynthetic rates, and 3–23% greater absolute relative growth rates in control treatments than for plants grown at low or high relative sea levels (Ellison and Farnsworth, 1997). Growth was also eventually reduced with increased levels of inundation, leading to the conclusion that any projected seedling or sapling growth benefit that may occur in response to a greater atmospheric supply of CO_2 with climate change might be offset by reduced growth of mangroves in response to longer hydroperiods and deeper flooding. Mangrove species from other locations have registered similar response; *K. candel* and *B. gymnorrhiza* grew rapidly over the first 2 months after sea-level rise simulations of 30 cm but were not able to maintain this rate beyond the initial period (Ye et al., 2004). Mangrove seedlings are fairly consistent in allocating more relative biomass to aboveground structures with prolonged flooding, but the degree to which this strategy serves to benefit mangrove seedling establishment and growth with rising sea-levels, altered nutrient regimes, and physico-chemical shifts remain uncertain. It is clear that continued seedling recruitment and adequate growth under persistent sea-level rise would warrant mangrove colonization of new intertidal areas (Sayed, 1995).

9. Biotic influences on environmental drivers

While a mangrove's fundamental niche may be defined by the physiological responses of its seedlings to microclimatological and edaphic conditions, direct and indirect interactions with other biota, especially crabs and insects, can play a large role in shaping a species' realized distribution, growth, and demography at early developmental stages. Other contributions to this special issue document the direct effects of consumers on mangrove recruitment and early growth, including the impacts of propagule predation by crabs and herbivory by leaf-feeding and stem-boring insects (Cannicci et al., 2008). Here, we examine: (1) how these plant–herbivore interactions may be mediated by local environmental conditions and (2) how modification of the soil physico-chemical environment by burrowing crabs can indirectly alter recruitment, establishment, and performance of mangrove seedlings.

9.1. Biota and local environmental conditions

The impact of arthropod consumers on the survival of mangrove propagules or seedlings has been demonstrated to vary with light/temperature conditions in several different systems. In an Australian forest on the northeast Queensland coast, Osborne and Smith (1990) found that rates of predation by crabs on tethered propagules of *A. marina* were higher in the understory than in adjacent canopy gaps, and declined with increasing light gap size. They attributed this pattern to a soil temperature-related shift in the distribution of crabs: herbivorous grapsid crabs, the most important propagule predators, were observed to be more abundant in the cooler microclimates of the understory and small gaps than in large gaps, where daytime soil temperatures are much higher. Working at another site in the same region of Australia, Clarke and Kerrigan (2002; see also Clarke, 2004) also measured lower rates of crab predation on tethered propagules in large light gaps than small ones or in the adjacent, shaded understory, and concluded that large gaps afford a refuge from crab predation for mangrove propagules. In contrast, a similar study on the Caribbean coast of Panama (Sousa and Mitchell, 1999) found no difference in crab predation rates between understory and gap environments and no relationship between canopy gap area and the rate of propagule predation by crabs. Daytime soil temperatures also increased with gap size at the latter site, but the crab species are different and may not respond in the same manner as Australian species to variation in conditions with gap size.

The effects of insect herbivores on seedling survival can also vary with light environment. Two independent studies, one on the Caribbean coast of Panama (Sousa et al., 2003b) and the other in the Florida Everglades (Devlin, 2004), have demonstrated that the stem-boring scolytid beetle, *Coccotrypes rhizophorae*, a specialist herbivore of *R. mangle*, causes much higher rates of seedling mortality in shaded understory environments than in light gaps. This predation prevents a layer of *R. mangle* saplings (i.e., advanced regeneration) from developing under a closed adult canopy; saplings of this species are largely restricted to light gaps and the areas immediately surrounding them. Why *R. mangle* seedlings are less vulnerable to beetle attack in gaps is not known. If female beetles disperse diurnally, they may avoid the high light intensity and temperatures characteristic of light gap environments. Alternatively, seedlings that establish in or near light gaps may undergo morphological or chemical changes that defend them against beetle attack.

9.2. Biotic modifications to the physico-chemical environment

In addition to the direct effects of their predation on mangrove propagules, crabs have been shown to exert strong indirect effects on mangrove seedling establishment, growth and survival through their bioturbation of sediments during burrow construction and maintenance. This activity can produce mounds of excavated sediment, altering both the topography and particle size of the substrate surface. This mechanism of mound formation was confirmed by Warren and Underwood's (1986) experimental manipulation of the burrowing ocypodid crab, *Heloecius cordiformis*, in a mangrove forest near Sydney, New South Wales, Australia. When crabs were added to enclosed areas of flat substrate, their burrowing significantly increased the height of the substrate surface by as much as 55 mm over the 129-day trial, as compared to control areas from which crabs were excluded. The presence of crabs also reduced the proportion of fine sediments (silts and clays) and increased the proportion of coarse sediment particles in the top 5 mm of substratum.

Minchinton (2001) examined the consequences of this mounded topography for recruitment of the mangrove, *A. marina*, at another site near Sydney, Australia. His study forest was also inhabited by a dense population of *H. cordiformis*. Mounds of crab-excavated sediment covered up to 44% of the forest floor, and these mounds were larger and comprised a greater proportion of the substratum under a closed canopy than in disturbance-generated light gaps. Crabs appeared to be less abundant in light gaps, perhaps because the sunlit gap environment is more thermally stressful than that of the shaded understory; this difference in crab density may have accounted for the smaller number and size of mounds inside gaps. Propagules and recently established seedlings of *A. marina* were also more abundant under the canopy than in gaps, and on flat areas surrounding mounds than on the mounds themselves. The greater density of propagules and young-of-the-year seedlings under the forest canopy was probably due to highly localized dispersal of propagules from parent trees. Directional dispersal of propagules accounted for the topographic effect. When experimentally placed on mounds, most propagules dispersed off them, onto the surrounding flats. The disproportionate numbers of propagules that accumulated in flat areas resulted in a higher density of seedlings in these areas than on mounds, despite the fact that the few propagules that remained on mounds established as rooted seedlings more quickly and at a three-fold higher rate than those that dispersed to the flats. Nonetheless, the more rapid establishment of propagules on mounds and apparently better growth conditions resulted in the tallest seedlings and saplings being most abundant on mounds within gaps. Minchinton (2001) hypothesized that the coarser grained sediments and higher density of crab burrows on mounds increase drainage, oxygenation and nutrient availability of these soils, creating better growth conditions for seedlings. Thus, the burrowing activity of crabs can have a marked indirect effect on spatial distribution of different age classes of juvenile mangroves across the forest floor.

An earlier study by Smith et al. (1991) in a *Rhizophora*-dominated mangrove forest in north Queensland, Australia provided strong evidence that changes in soil chemistry due to crab burrowing can benefit mangrove seedlings. When the density of burrowing grapsid crabs was reduced by pitfall-trapping, concentrations of soil sulfide and ammonium increased significantly and stand productivity (estimated by stipule and propagule production) declined, compared to control plots. The changes in soil chemistry were attributed to a reduction in soil aeration as the density of crab burrows declined. While there is a critical need to replicate this study at other sites, it appears that crab burrowing and associated bioturbation of sediments can indirectly enhance mangrove forest productivity and seedling growth. Similarly, burrowing by fiddler crabs (*Uca* spp., Ocypodidae) has been shown to increase soil drainage and aeration, alter sediment chemistry, and increase aboveground plant productivity in temperate salt marshes where these crabs excavate extensive burrow systems (Montague, 1982; Bertness, 1985).

10. Conclusions

In this review, we took a comprehensive approach to describing the effects that multiple ecological factors may have on seedling ecophysiology and growth in mangroves. We discussed old ideas and new advances in our understanding of how salinity, light, nutrients, and flooding impact mangrove seedling establishment, and have indicated a principal research need for interactive studies. We have also explained how biota can affect the soil physico-chemical environment and influence seedling establishment indirectly. What is especially new to this review, however, is that we identified the importance of non-traditional factors – temperature, CO_2, and sea-level rise – as important drivers not only to mangrove establishment on a global scale, but also to seedling growth and persistence on a local scale. Research should attempt to include these factors along with potentially more subservient site-specific factors of salinity, light, nutrients, and flooding in future evaluations.

The last two decades have witnessed the destruction of 35% of the earth's mangrove forests (Valiela et al., 2001). In order to ensure that specific mangrove locations will remain intact over the next two decades, seedling establishment in environments conducive to early development will need to be ensured. Our review underscores some of the critical global and local factors responsible for dictating seedling success in diverse intertidal locations.

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References

Allen, J.A., Krauss, K.W., Hauff, R.D., 2003. Factors limiting the intertidal distribution of the mangrove species *Xylocarpus granatum*. Oecologia 135, 110–121.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Andrews, T.J., Clough, B.F., Muller, G.J., 1984. Photosynthetic gas exchange properties and carbon isotope ratios of some mangroves in North Queensland. In: Teas, H.J. (Ed.), Biology and Ecology of Mangroves. Tasks in Vegetation Science, vol. 8. Dr. W. Junk Publishers, The Netherlands, pp. 15–23.

Aziz, I., Khan, M.A., 2001. Experimental assessment of salinity tolerance of *Ceriops tagal* seedlings and saplings from the Indus delta Pakistan. Aquat. Bot. 70, 259–268.

Ball, M.C., 1980. Patterns of secondary succession in a mangrove forest of southern Florida. Oecologia 44, 226–235.

Ball, M.C., 1986. Photosynthesis in mangroves. Wetlands (Australia) 6, 12–22.

Ball, M.C., 1988a. Ecophysiology of mangroves. Trees 2, 129–142.

Ball, M.C., 1988b. Salinity tolerance in the mangroves *Aegiceras corniculatum* and *Avicennia marina*. I. Water use in relation to growth, carbon partitioning and salt balance. Aust. J. Plant Physiol. 15, 447–464.

Ball, M.C., 1996. Comparative ecophysiology of mangrove forest and tropical lowland moist rainforest. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Chapman and Hall, New York, pp. 461–496.

Ball, M.C., 1998. Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River floodplain, northern Australia. Global Ecol. Biogeogr. Lett. 7, 73–82.

Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. Trees Struct. Funct. 16, 126–139.

Ball, M.C., Anderson, J.M., 1986. Sensitivity of Photosystem II to NaCl in relation to salinity tolerance. Comparative studies with thylakoids of the salt-tolerant mangrove, *Avicennia marina* and the salt-sensitive pea, *Pisum sativum*. Aust. J. Plant Physiol. 13, 689–698.

Ball, M.C., Chow, W.S., Anderson, J.M., 1987. Salinity-induced potassium deficiency causes loss of functional Photosystem II in leaves of the grey mangrove, *Avicennia marina*, through depletion of the atrazine-binding polypeptide. Aust. J. Plant Physiol. 14, 351–361.

Ball, M.C., Cochrane, M.J., Rawson, H.M., 1997. Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO_2. Plant Cell Environ. 20, 1158–1166.

Ball, M.C., Cowan, I.R., Farquhar, G.D., 1988. Maintenance of leaf temperature and the optimisation of carbon gain in relation to water loss in a tropical mangrove forest. Aust. J. Plant Physiol. 15, 263–276.

Ball, M.C., Critchley, C., 1982. Photosynthetic responses to irradiance by the grey mangrove, *Avicennia marina*, grown under different light regimes. Plant Physiol. 70, 1101–1106.

Ball, M.C., Farquhar, G.D., 1984. Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. Plant Physiol. 74, 1–6.

Ball, M.C., Munns, R., 1992. Plant response to salinity under elevated atmospheric concentration of CO_2. Aust. J. Bot. 40, 515–525.

Ball, M.C., Passioura, J.B., 1994. Carbon gain in relation to water use. In: Schulze, E.D., Caldwell, N.M. (Eds.), Ecophysiology of Photosynthesis. Springer, Heidelberg, pp. 247–257.

Ball, M.C., Pidsley, S.M., 1995. Growth responses to salinity in relation to distribution of two mangrove species, *Sonneratia alba* and *S. lanceolata,* in northern Australia. Funct. Ecol. 9, 77–85.

Bashan, Y., Holguin, G., 2002. Plant growth-promoting bacteria: a potential tool for arid mangrove reforestation. Trees Struct. Funct. 16, 159–166.

Bazzaz, F.A., 1990. The response of natural ecosystems to the rising global CO_2 levels. Annu. Rev. Ecol. Syst. 21, 167–196.

Berger, U., Adams, M., Grimm, V., Hildenbrandt, H., 2006. Modelling secondary succession of neotropical mangroves: causes and consequences of growth reduction in pioneer species. Pers. Plant Ecol. Evol. Syst. 7, 243–252.

Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modeling of forest dynamics: spacing, ageing and neighborhood competition of mangrove trees. Ecol. Modell. 132, 287–302.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Bertness, M.D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology 66, 1042–1055.

Biber, P.D., 2006. Measuring the effects of salinity stress in the red mangrove *Rhizophora mangle* L. Afr. J. Agric. Res. 1, 1–4.

Björkman, O., Demmig, B., Andrews, T.J., 1988. Mangrove photosynthesis: response to high-irradiance stress. Aust. J. Plant Physiol. 15, 43–61.

Blair, B.C., Perfecto, I., 2001. Nutrient content and substrate effect on fine root density and size distribution in a Nicaraguan rain forest. Biotropica 33, 697–701.

Boto, K.G., Saffigna, P., Clough, B., 1985. Role of nitrate in nitrogen nutrition of the mangrove *Avicennia marina*. Mar. Ecol. Prog. Ser. 21, 259–265.

Boto, K.G., Wellington, J.T., 1983. Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest. Mar. Ecol. Prog. Ser. 11, 63–69.

Bouwer, R., 1962. Nutritive influences on the distribution of dry matter in the plant. Neth. J. Agric. Sci. 10, 361–376.

Britto, D.T., Siddiqi, M.Y., Glass, A.D.M., Kronzucker, H.J., 2001. Futile transmembrane NH_4^+ cycling: a cellular hypothesis to explain ammonium toxicity in plants. Proc. Nat. Acad. Sci. USA 98, 4255–4258.

Burchett, M.D., Clarke, C.J., Field, C.D., Pulkownik, A., 1989. Growth and respiration in two mangrove species at a range of salinities. Physiol. Plant. 75, 299–303.

Burchett, M.D., Field, C.D., Pulkownik, A., 1984. Salinity, growth and root respiration in the grey mangrove *Avicennia marina*. Physiol. Plant. 60, 113–118.

Camilleri, J.C., Ribi, G., 1983. Leaf thickness of mangroves (*Rhizophora mangle*) growing in different salinities. Biotropica 15, 139–141.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Cardona-Olarte, P., Twilley, R.R., Krauss, K.W., Rivera-Monroy, V.H., 2006. Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. Hydrobiologia 569, 325–341.

Chapin III, F.S., 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11, 233–260.

Chapin III, F.S., 1991. Effects of multiple environmental stresses on nutrient availability and use. In: Mooney, H.A., Winner, W., Pell, E.J. (Eds.), Responses of Plants to Multiple Stresses. Academic Press Inc., San Diego, pp. 67–88.

Chapin III, F.S., Bloom, A.J., Field, C.B., Waring, R.H., 1987. Plant responses to multiple environmental factors. BioScience 37, 49–57.

Chapman, V.J., 1976. Mangrove Vegetation. J. Cramer, Vaduz, Germany.

Cheeseman, J.M., 1991. The analysis of photosynthetic performance in leaves under field conditions: a case study using *Bruguiera* mangroves. Photosynth. Res. 29, 11–22.

Cheeseman, J.M., Herendeen, L.B., Cheeseman, A.T., Clough, B.F., 1997. Photosynthesis and photoprotection in mangroves under field conditions. Plant Cell Environ. 20, 579–588.

Chen, R., Twilley, R.R., 1998. A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. J. Ecol. 86, 37–52.

Chen, R., Twilley, R.R., 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. Estuaries 22, 955–970.

Chen, L.Z., Wang, W.Q., Lin, P., 2004. Influence of waterlogging time on the growth of *Kandelia candel* seedlings. Acta Oceanol. Sin. 23, 149–158.

Chen, L.Z., Wang, W.Q., Lin, P., 2005. Photosynthetic and physiological responses of *Kandelia candel* L. Druce seedlings to duration of tidal immersion in artificial seawater. Environ. Exp. Bot. 54, 256–266.

Christian, R., 2005. Interactive effects of salinity and irradiance on photoprotection in acclimated seedlings of two sympatric mangroves. Trees 19, 596–606.

Clarke, P.J., 2004. Effects of experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. J. Ecol. 92, 203–213.

Clarke, P.J., Allaway, W.G., 1993. The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light, and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.

Clark, R.L., Guppy, J.C., 1988. A transition from mangrove forest to freshwater wetland in the monsoon tropics of Australia. J. Biogeogr. 15, 665–684.

Clarke, P.J., Kerrigan, R.A., 2000. Do forest gaps influence the population structure and species composition of mangrove stands in northern Australia? Biotropica 32, 642–652.

Clarke, P.J., Kerrigan, R.A., 2002. The effects of seed predators on the recruitment of mangroves. J. Ecol. 90, 728–736.

Clough, B.F., 1984. Growth and salt balance of the mangroves *Avicennia marina* (Forsk) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. Aust. J. Plant Physiol. 11, 419–430.

Clough, B.F., 1992. Primary productivity and growth of mangrove forests. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, pp. 225–249.

Clough, B.F., Sim, R.G., 1989. Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. Oecologia 79, 38–44.

Corlett, R.T., 1986. The mangrove understory: some additional observations. J. Trop. Ecol. 2, 93–94.

Cram, W.J., Torr, P.G., Rose, D.A., 2002. Salt allocation during leaf development and leaf fall in mangroves. Trees 16, 112–119.

Dahdouh-Guebas, F., DeBondt, R., Abeysinghe, P.D., Kairo, J.G., Cannicci, S., Triest, L., Koedam, N., 2004. Comparative study of the disjunct zonation pattern of the grey mangrove *Avicennia marina* (Forsk) Vierh. in Gazi Bay (Kenya). Bull. Mar. Sci. 74, 237–252.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Verneirt, M., Cannicci, S., Kairo, J.G., Tack, J.F., Koedam, N., 2002. An exploratory study on grapsid crab zonation in Kenyan mangroves. Wetlands Ecol. Manage. 10, 179–187.

Devlin, D.J., 2004. Analyses of the Relationship between a Parasitic Beetle (*Coccotrypes rhizophorae*) and a Host Plant, the Red Mangrove (*Rhizophora mangle*). Dissertation, University of Louisiana at Lafayette.

Duke, N.C., 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. Wetlands Ecol. Manage. 9, 257–269.

Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecol. Biogeogr. Lett. 7, 27–47.

Ellison, A.M., Farnsworth, E.J., 1993. Seedling survivorship, growth, and response to disturbance in Belizean mangal. Am. J. Bot. 80, 1137–1145.

Ellison, A.M., Farnsworth, E.J., 1997. Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L). Oecologia 112, 435–446.

Ellison, A.M., Farnsworth, E.J., Twilley, R.R., 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77, 2431–2444.

Ellison, A.M., Mukherjee, B.B., Karim, S., 2000. Testing patterns of zonation in mangroves: scale-dependence and environmental correlates in the Sundarbans of Bangladesh. J. Ecol. 88, 813–824.

Ewel, K.C., Bourgeois, J.A., Cole, T.G., Zheng, S., 1998b. Variation in environmental characteristics and vegetation in high-rainfall mangrove forests, Kosrae Micronesia. Global Ecol. Biogeogr. Lett. 7, 49–56.

Ewel, K.C., Cressa, C., Kneid, R.T., Lake, P.S., Levin, L.A., Palmer, M.A., Snelgrove, P., Wall, D.H., 2001. Managing critical transition zones. Ecosystems 4, 452–460.

Ewel, K.C., Twilley, R.R., Ong, J.E., 1998a. Different kinds of mangrove forests provide different goods and services. Global Ecol. Biogeogr. Lett. 7, 83–94.

Ewel, K.C., Zheng, S., Pinzón, Z.S., Bourgeois, J.A., 1998c. Environmental effects of canopy gap formation in high-rainfall mangrove forests. Biotropica 30, 510–518.

Farnsworth, E.J., Ellison, A.M., Gong, W.K., 1996. Elevated CO_2 alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L). Oecologia 108, 599–609.

Farquhar, G.D., Ball, M.C., von Caemmerer, S., Roksandic, Z., 1982. Effect of salinity and humidity on δ^{13}C values of halophytes: evidence for differential isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia 52, 121–137.

Feller, I.C., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecol. Monogr. 65, 477–505.

Feller, I.C., Lovelock, C.E., McKee, K.L., 2007. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen vs. phosphorus limited mangrove. Ecosystems 10, 347–359.

Feller, I.C., McKee, K.L., 1999. Small gap creation in Belizean mangrove forests by a wood-boring insect. Biotropica 31, 607–617.

Feller, I.C., Whigham, D.F., McKee, K.L., Lovelock, C.E., 2003. Nitrogen limitation of growth and nutrient dynamics in a mangrove forest, Indian River Lagoon, Florida. Oecologia 134, 405–414.

Feller, I.C., Whigham, D.F., McKee, K.L., O'Neill, J.P., 2002. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62, 145–175.

Field, C.D., 1984. Movement of ions and water into the xylem sap of tropical mangroves. In: Teas, H.J. (Ed.), Biology and Ecology of Mangroves. Tasks in Vegetation Science, vol. 8. Dr. W. Junk Publishers, The Netherlands, pp. 49–52.

Field, C., Merino, J., Mooney, H.A., 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of Californian evergreens. Oecologia 60, 384–389.

Field, C.B., Mooney, H.A., 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish, T.J. (Ed.), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, pp. 25–55.

Flowers, T.J., Troke, P.F., Yeo, A.R., 1977. The mechanism of salt tolerance in halophytes. Annu. Rev. Plant Physiol. 28, 89–121.

Flowers, T.J., Yeo, A.R., 1986. Ion relations of plants under drought and salinity. Aust. J. Plant Physiol. 13, 75–91.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Grime, J.P., 1979. Plant Strategies and Vegetation Strategies. John Wiley and Sons, Chichester.

He, B., Lai, T., Fan, H., Wang, W., Zheng, H., 2007. Comparison of flooding-tolerance in four mangrove species in a diurnal tidal zone in the Beibu Gulf. Estuarine Coast. Shelf Sci. 74, 254–262.

Hodge, A., 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol. 162, 9–24.

Hogarth, P.J., 1999. The Biology of Mangroves. Oxford University Press, Oxford.

Hsueh, M., Lee, H., 2000. Diversity and distribution of the mangrove forests in Taiwan. Wetlands Ecol. Manage. 8, 233–242.

Hutchings, P.A., Saenger, P., 1987. Ecology of Mangroves. University of Queensland Press, St. Lucia, Queensland, Australia.

IPCC, 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York.

Janzen, D.H., 1985. Mangroves: where's the understory? J. Trop. Ecol. 1, 89–92.

Kao, W.Y., Shih, C.N., Tsai, T.T., 2004. Sensitivity to chilling temperatures and distribution differ in the mangrove species *Kandelia candel* and *Avicennia marina*. Tree Physiol. 24, 859–864.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. Adv. Mar. Biol. 40, 81–251.

Kitaya, Y., Jintana, V., Piriyayotha, S., Jaijing, D., Yabuki, K., Izutani, S., Nishimiya, A., Iwasaki, M., 2002. Early growth of seven mangrove species planted at different elevations in a Thai estuary. Trees 16, 150–154.

Koch, M.S., 1996. Resource Availability and Abiotic Effects on *Rhizophora mangle* L. (Red Mangrove) Development in South Florida. Dissertation, University of Miami, Coral Gables.

Koch, M.S., 1997. *Rhizophora mangle* L. seedling development into the sapling stage across resource and stress gradients in subtropical Florida. Biotropica 29, 427–439.

Koch, M.S., Snedaker, S.C., 1997. Factors influencing *Rhizophora mangle* L. seedling development in Everglades carbonate soils. Aquat. Bot. 59, 87–98.

Komiyama, A., Havanond, S., Srisawatt, W., Mochida, Y., Fujimoto, K., Ohnishi, T., Ishihara, S., Miyagi, T., 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr) C. B. Rob.) forest. Forest Ecol. Manage. 139, 127–134.

Kothamasi, D., Kothamasi, S., Bhattacharyya, A., Chander Kuhad, R., Babu, C.R., 2006. Arbuscular mycorrhizae and phosphate solubilising bacteria of the rhizosphere of the mangrove ecosystem of Great Nicobar island, India. Biol. Fertil. Soils 42, 358–361.

Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. Monogr. 1, 1–29.

Krauss, K.W., Allen, J.A., 2003a. Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. Aquat. Bot. 77, 311–324.

Krauss, K.W., Allen, J.A., 2003b. Factors influencing the regeneration of the mangrove *Bruguiera gymnorrhiza* (L) Lamk. on a tropical Pacific island. Forest Ecol. Manage. 176, 49–60.

Krauss, K.W., Doyle, T.W., Twilley, R.R., Rivera-Monroy, V.H., Sullivan, J.K., 2006b. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. Hydrobiologia 569, 311–324.

Krauss, K.W., Twilley, R.R., Doyle, T.W., Gardiner, E.S., 2006a. Leaf gas exchange characteristics of three neotropical mangrove species in response to varying hydroperiod. Tree Physiol. 26, 959–968.

Krauss, K.W., Young, P.J., Chambers, J.L., Doyle, T.W., Twilley, R.R., 2007. Sap flow characteristics of neotropical mangroves in flooded and drained soils. Tree Physiol. 27, 775–783.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Lahmann, E.J., 1988. Effects of Different Hydrological Regimes on the Productivity of *Rhizophora mangle* L.: A Case Study of Mosquito Control Impoundments at Hutchinson Island, Saint Lucie County, Florida. Dissertation, University of Miami.

Lambers, H., Chapin III, F.S., Pons, T.L., 1998. Plant Physiological Ecology. Springer, Berlin, Heidelberg, New York.

Larcher, W., 2001. Physiological Plant Ecology, fourth ed. Springer, Berlin.

Lin, G., Sternberg, L.da S.L., 1992. Effects of growth form, salinity, nutrient, and sulphide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L). Aust. J. Plant Physiol. 19, 509–517.

Lin, G., Sternberg, L.da S.L., 1995. Variation in propagule mass and its effect on carbon assimilation and seedling growth of red mangrove (*Rhizophora mangle*) in Florida USA. J. Trop. Ecol. 11, 109–119.

López-Hoffman, L., Ackerly, D.D., Anten, N.P.R., DeNoyer, J.L., Martínez-Ramos, M., 2007b. Gap-dependence in mangrove life-history strategies: A consideration of the entire life cycle and patch dynamics. J. Ecol. 95, 1222–1233.

López-Hoffman, L., Anten, N.P.R., Martínez-Ramos, M., Ackerly, D., 2007a. Salinity and light interactively affect neotropical mangrove seedlings at the leaf and whole plant levels. Oecologia 150, 545–556.

López-Hoffman, L., DeNoyer, J.L., Monroe, I.E., Shaftel, R., Anten, N.P.R., Martínez-Ramos, M., Ackerly, D.D., 2006. Mangrove seedling net photosynthesis, growth, and survivorship are interactively affected by salinity and light. Biotropica 38, 606–616.

Lovelock, C.E., Ball, M.C., Choat, B., Engelbrecht, B.M.J., Holbrook, N.M., Feller, I.C., 2006a. Linking physiological processes with mangrove forest structure: phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. Plant Cell Environ. 29, 793–802.

Lovelock, C.E., Clough, B.F., 1992. Influence of solar radiation and leaf angle on leaf xanthophyll concentrations in mangroves. Oecologia 91, 518–525.

Lovelock, C.E., Clough, B.F., Woodrow, I.E., 1992. Distribution and accumulation of ultraviolet-radiation-absorbing compounds in leaves of tropical mangroves. Planta 188, 143–154.

Lovelock, C.E., Feller, I.C., 2003. Photosynthetic performance and resource utilization of two mangrove species coexisting in hypersaline scrub forest. Oecologia 134, 455–462.

Lovelock, C.E., Feller, I.C., Ellis, J., Hancock, N., Schwarz, A.M., Sorrell, B., 2007. Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. Oecologia 153, 633–641.

Lovelock, C.E., Feller, I.C., McKee, K.L., Engelbrecht, B.M., Ball, M.C., 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. Funct. Ecol. 18, 25–33.

Lovelock, C.E., Feller, I.C., McKee, K.L., Thompson, R., 2005. Variation in mangrove forest structure and sediment characteristics in Bocas del Toro Republic of Panamá. Caribb. J. Sci. 41, 456–464.

Lovelock, C.E., Ruess, R.W., Feller, I.C., 2006b. Root respiration in *Rhizophora mangle* over variation in forest stature and nutrient availability. Tree Physiol. 26, 1601–1606.

Lugo, A.E., 1986. Mangrove understory: as expensive luxury? J. Trop. Ecol. 2, 287–288.

Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. 5, 39–64.

Lugo, A.E., Zucca, C.P., 1977. The impact of low temperature stress on mangrove structure and growth. Trop. Ecol. 18, 149–161.

Lüttge, U., 1997. Physiological Ecology of Tropical Plants. Springer-Verlag, New York.

Markley, J.L., McMillan, C., Thompson Jr., G.A., 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. Can. J. Bot. 60, 2704–2715.

Mazda, Y., Yokochi, H., Sato, Y., 1990. Groundwater flow in the Bashita-Minato mangrove area, and its influence on water and bottom mud properties. Estuarine Coast. Shelf Sci. 31, 621–638.

McGuinness, K.A., 1997. Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. Oecologia 109, 80–87.

McKee, K.L., 1993. Soil physicochemical patterns and mangrove species distribution – reciprocal effects? J. Ecol. 81, 477–487.

McKee, K.L., 1995. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. Am. J. Bot. 82, 299–307.

McKee, K.L., 1996. Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia. Tree Physiol. 16, 883–889.

McKee, K.L., 2001. Root proliferation in decaying roots and old root channels: a nutrient conservation mechanism in oligotrophic mangrove forests? J. Ecol. 89, 876–887.

McKee, K.L., 2006. Where temperate meets tropical: relative responses of salt marsh and mangrove species to nitrogen and CO_2 enrichment. In: Society of Wetland Scientists 27th International Conference, Cairns, Australia, pp. 83–84.

McKee, K.L., Feller, I.C., Popp, M., Wanek, W., 2002. Mangrove isotopic (δ^{15}N and δ^{13}C) fractionation across a nitrogen vs. phosphorus limitation gradient. Ecology 83, 1065–1075.

McKee, K.L., Mendelssohn, I.A., 1987. Root metabolism in the black mangrove (*Avicennia germinans* (L) L.): response to hypoxia. Environ. Exp. Bot. 27, 147–156.

McKee, K.L., Mendelssohn, I.A., Hester, M.W., 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. Am. J. Bot. 75, 1352–1359.

McMillan, C., 1971. Environmental factors affecting seedling establishment of the black mangrove on the central Texas coast. Ecology 52, 927–930.

McMillan, C., Sherrod, C.L., 1986. The chilling tolerance of black mangrove, *Avicennia germinans*, from the Gulf of Mexico coast of Texas Louisiana and Florida. Contrib. Mar. Sci. 29, 9–16.

Medina, E., Francisco, M., 1997. Osmolality and delta-13C of leaf tissues of mangrove species from environments of contrasting rainfall and salinity. Estuarine Coast. Shelf Sci. 45, 337–344.

Medina, E., Lugo, A., Novelo, A., 1995. Contenido mineral del tejido foliar de especies de manglar de la Laguna Santecomapan (Veracruz Mexico) y su relacion con la salinidad. Biotropica 27, 317–323.

Middleton, B.A., McKee, K.L., 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J. Ecol. 89, 818–828.

Minchinton, T.E., 2001. Canopy and substratum heterogeneity influence recruitment of the mangrove *Avicennia marina*. J. Ecol. 89, 888–902.

Montague, C.L., 1982. In: Kennedy, V.S. (Ed.), The Influence of Fiddler Crab Burrows and Burrowing on Metabolic Processes in Salt Marsh Sediments. Estuarine Comparisons Academic, New York, pp. 283–301.

Moon, G.J., Clough, B.F., Peterson, C.A., Allaway, W.G., 1986. Apoplastic and symplastic pathways in *Avicennia marina* (Forsk) Vierh. roots revealed by fluorescent tracer dyes. Aust. J. Plant Physiol. 13, 637–648.

Munns, R., 2002. Comparative physiology of salt and water stress. Plant Cell Environ. 25, 239–250.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Naidoo, G., 1983. Effects of flooding on leaf water potential and stomatal resistance in *Bruguiera gymnorrhiza* (L) Lam. New Phytol. 93, 369–376.

Naidoo, G., 1985. Effects of waterlogging and salinity on plant–water relations and on the accumulation of solutes in three mangrove species. Aquat. Bot. 22, 133–143.

Naidoo, G., 1987. Effects of salinity and nitrogen on growth and water relations in the mangrove *Avicennia marina* (Forsk.) Vierh. New Phytol. 107, 317–325.

Naidoo, G., 2006. Factors contributing to dwarfing in the mangrove *Avicennia marina*. Ann. Bot. 97, 1095–1101.

Naidoo, G., Rogalla, H., von Willert, D.J., 1997. Gas exchange responses of a mangrove species, *Avicennia marina*, to waterlogged and drained conditions. Hydrobiologia 352, 39–47.

Naidoo, G., Tuffers, A.V., von Willert, D.J., 2002. Changes in gas exchange and chlorophyll fluorescence characteristics of two mangroves and a mangrove associate in response to salinity in the natural environment. Trees 16, 140–146.

Norman, H.A., McMillan, C., Thompson, G.A., 1984. Phosphatidylglycerol molecular species in chilling-sensitive and chilling-resistant populations of *Avicennia germanans* (L) L. Plant Cell Physiol. 25, 1437–1444.

Odum, W.E., McIvor, C.C., Smith, T.J., III, 1982. The Ecology of the Mangroves of South Florida: A Community Profile. FWS/OBS-81/24, U.S. Fish and Wildlife Service, Washington.

Onuf, C.P., Teal, J.M., Valiela, I., 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58, 514–526.

Osborne, K., Smith III, T.J., 1990. Differential predation on mangrove propagules in open and closed canopy forest habitats. Vegetatio 89, 1–6.

Osmond, C.B., 1994. What is photoinhibition? Some insights from comparisons of shade and sun plants. In: Baker, N.R., Bowyer, J.R. (Eds.), Photoinhibition of Photosynthesis. Bios Scientific, Oxford, pp. 1–24.

Osunkoya, O.O., Creese, R.G., 1997. Population structure, spatial pattern and seedling establishment of the grey mangrove, *Avicennia marina* var. *australasica*, in New Zealand. Aust. J. Bot. 45, 707–725.

Ovalle, A.R.C., Rezende, C.E., Lacerda, L.D., Silva, C.A.R., 1990. Factors affecting the hydrochemistry of a mangrove tidal creek, Sepetiba Bay, Brazil. Estuarine Coast. Shelf Sci. 31, 639–650.

Paliyavuth, C., Clough, B., Patanaponpaiboon, P., 2004. Salt uptake and shoot water relations in mangroves. Aquat. Bot. 78, 349–360.

Passioura, J.B., Ball, M.C., Knight, J.H., 1992. Mangroves may salinize the soil and in so doing limit their transpiration rate. Funct. Ecol. 6, 476–481.

Pezeshki, S.R., DeLaune, R.D., Meeder, J.F., 1997. Carbon assimilation and biomass partitioning in *Avicennia germinans* and *Rhizophora mangle* seedlings in response to soil redox conditions. Environ. Exp. Bot. 37, 161–171.

Pezeshki, S.R., DeLaune, R.D., Patrick Jr., W.H., 1989. Effects of fluctuating rhizosphere redox potential on carbon assimilation of *Spartina alterniflora*. Oecologia 80, 132–135.

Pezeshki, S.R., DeLaune, R.D., Patrick Jr., W.H., 1990. Differential response of selected mangroves to soil flooding and salinity: gas exchange and biomass. Can. J. Forest Res. 20, 869–874.

Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Aust. J. Plant Physiol. 27, 595–607.

Poorter, H., Navas, M.L., 2003. Plant growth and competition at elevated CO_2: on winners, losers and functional groups. New Phytol. 157, 175–198.

Poorter, H., VanBerkel, Y., Baxter, R., DenHertog, J., Dijkstra, P., Gifford, R.M., Griffin, K.L., Roumet, C., Roy, J., Wong, S.C., 1997. The effect of elevated CO_2 on the chemical composition and construction costs of leaves of 27 C_3 species. Plant Cell Environ. 20, 472–482.

Popp, M., 1995. Salt resistance in herbaceous halophytes and mangroves. Prog. Bot. 56, 416–429.

Popp, M., Larher, F., Weigel, P., 1984. Chemical composition of Australian mangroves. III. Free amino acids, total methylated onium compounds and total nitrogen. Z. Pflanzenphysiol. 114, 15–25.

Popp, M., Polania, J., 1989. Compatible solutes in different organs of mangrove trees. Ann. Sci. For. 46, 842s–844s.

Popp, M., Polania, J., Weiper, M., 1993. Physiological adaptations to different salinity levels in mangroves. In: Leith, H., Al Masoom, A. (Eds.), Towards the Rational Use of High Salinity Tolerant Plants, vol. 1. Kluwer Academic Publishers, The Netherlands, pp. 217–224.

Putz, F.E., Chan, H.T., 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. Forest Ecol. Manage. 17, 211–230.

Rabinowitz, D., 1978a. Early growth of mangrove seedlings in Panamá, and an hypothesis concerning the relationship of dispersal and zonation. J. Biogeogr. 5, 113–133.

Rabinowitz, D., 1978b. Dispersal properties of mangrove propagules. Biotropica 10, 47–57.

Rao, R.G., Woitchik, A.F., Goeyens, L., van Riet, A., Kazungu, J., Dehairs, F., 1994. Carbon, nitrogen contents and stable carbon isotope abundance in mangrove leaves from an east African coastal lagoon (Kenya). Aquat. Bot. 47, 175–183.

Robertson, A.I., Alongi, D.M. (Eds.), 1992. Tropical Mangrove Ecosystems. Coastal and Estuarine Studies 41, American Geophysical Union, Washington.

Rojas, A., Holguin, G., Glick, B.R., Bashan, Y., 2001. Synergism between *Phyllobacterium* sp. (N_2-fixer) and *Bacillus licheniformis* (P-solubilizer), both from a semiarid mangrove rhizosphere. FEMS Microbiol. Ecol. 35, 181–187.

Saenger, P., 2002. Mangrove Ecology Silviculture and Conservation. Kluwer Academic Publishers, Dordrecht.

Saenger, P., Specht, M.M., Specht, R.L., Chapman, V.J., 1977. Mangal and coastal salt marsh communities. In: Chapman, V.J. (Ed.), Wet Coastal Environments. Elsevier, Amsterdam, pp. 293–345.

Sakai, A., Wardle, P., 1978. Freezing resistance of New Zealand trees and shrubs. N. Z. J. Ecol. 1, 51–61.

Saxe, H., Ellsworth, D.S., Heath, J., 1998. Tree and forest functioning in an enriched CO_2 atmosphere. New Phytol. 139, 395–436.

Sayed, O.H., 1995. Effects of the expected sea level rise on *Avicennia marina* L: a case study in Qatar. Qatar Univ. Sci. J. 15, 91–94.

Schaeffer-Novelli, Y., Cintrón-Molero, G., Adaime, R.R., Camargo, T.M., 1990. Variablility of mangrove ecosystems along the Brazilian Coast. Estuaries 13, 204–218.

Scholander, P.F., 1968. How mangroves desalinate seawater. Physiol. Plant. 21, 251–261.

Scholander, P.F., Bradstreet, E.D., Hammel, H.T., Hemmingsen, E.A., 1966. Sap concentrations in halophytes and some other plants. Plant Physiol. 41, 529–532.

Scholander, P.F., Hammel, H.T., Hemmingsen, E.A., Garay, W., 1962. Salt balance in mangroves. Plant Physiol. 37, 722–729.

Semeniuk, V., 1983. Mangrove distribution in northwestern Australia in relationship to regional and local freshwater seepage. Vegetatio 53, 11–31.

Semeniuk, V., 1994. Predicting the effect of sea-level rise on mangroves of northwestern Australia. J. Coast Res. 10, 1050–1076.

Sengupta, A., Chaudhuri, S., 2002. Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. Mycorrhiza 12, 169–174.

Sherman, R.E., Fahey, T.J., Battles, J.J., 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. J. Ecol. 88, 165–178.

Sherman, R.E., Fahey, T.J., Howarth, R.W., 1998. Soil-plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. Oecologia 115, 553–563.

Sherrod, C.L., Hockaday, D.L., McMillan, C., 1986. Survival of red mangrove, *Rhizophora mangle*, on the Gulf of Mexico coast of Texas. Contrib. Mar. Sci. 29, 27–36.

Sherrod, C.L., McMillan, C., 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. Contrib. Mar. Sci. 28, 129–140.

Skelton, N.J., Allaway, W.G., 1996. Oxygen and pressure changes measured in situ during flooding in roots of the gray mangrove *Avicennia marina* (Forssk) Vierh. Aquat. Bot. 54, 165–175.

Smith III, T.J., 1987a. Seed predation in relation to dominance and distribution in mangrove forests. Ecology 68, 266–273.

Smith III, T.J., 1987b. Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. Estuarine Coast. Shelf Sci. 25, 43–51.

Smith III, T.J., 1987c. Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. J. Exp. Mar. Biol. Ecol. 110, 133–146.

Smith III, T.J., 1988. Differential distribution between sub-species of the mangrove *Ceriops tagal*: competitive interactions along a salinity gradient. Aquat. Bot. 32, 79–89.

Smith III, T.J., 1992. Forest structure. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. Coastal and Estuarine Studies 41. American Geophysical Union, Washington, pp. 101–136.

Smith III, T.J., Boto, K.G., Frusher, S.D., Giddins, R.L., 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuarine Coast. Shelf Sci. 33, 419–432.

Smith, J.A.C., Popp, M., Lüttge, U., Cram, W.J., Diaz, M., Griffiths, H., Lee, H.S.J., Medina, E., Schäfer, C., Stimmel, K.-H., Thonke, B., 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. VI. Water relations and gas exchange of mangroves. New Phytol. 111, 293–307.

Smith III, T.J., Robblee, M.B., Wanless, H.R., Doyle, T.W., 1994. Mangroves, hurricanes, and lightening strikes: assessment of Hurricane Andrew suggests and interaction across two differing scales of disturbance. BioScience 44, 256–262.

Smith, S.M., Snedaker, S.C., 1995. Salinity responses in two populations of viviparous *Rhizophora mangle* L. seedlings. Biotropica 27, 435–440.

Snedaker, S.C., Araujo, R.J., 1998. Stomatal conductance and gas exchange in four species of Caribbean mangroves exposed to ambient and increased CO_2. Mar. Freshwater Res. 49, 325–327.

Snedaker, S.C., Lahmann, E.J., 1988. Mangrove understorey absence: a consequence of evolution? J. Trop. Ecol. 4, 311–314.

Sobrado, M.A., 1999. Leaf photosynthesis of the mangrove *Avicennia germinans* as affected by NaCl. Photosynthetica 36, 547–555.

Sobrado, M.A., 2000. Relation of water transport to leaf gas exchange properties in three mangrove species. Trees 14, 258–262.

Sobrado, M.A., 2001. Hydraulic properties of a mangrove *Avicennia germinans* as affected by NaCl. Biol. Plant. 44, 435–438.

Sobrado, M.A., 2005. Leaf characteristics and gas exchange of the mangrove *Laguncularia racemosa* as affected by salinity. Photosynthesis 43, 217–221.

Sobrado, M.A., Ball, M.C., 1999. Light use in relation to carbon gain in the mangrove, *Avicennia marina*, under hypersaline conditions. Aust. J. Plant Physiol. 26, 245–251.

Sobrado, M.A., Ewe, S.M.L., 2006. Linking hypersalinity to leaf physiology in *Avicennia germinans* and *Laguncularia racemosa* coexisting in a scrub mangrove forest at the Indian River Lagoon Florida. Trees 20, 679–687.

Sobrado, M.A., Greaves, E., 2000. Leaf secretion composition of the mangrove species *Avicennia germinans* (L) in relation to salinity: a case study by using total-reflection X-ray fluorescence analysis. Plant Sci. 159, 1–5.

Sousa, W.P., Kennedy, P.G., Mitchell, B.J., 2003a. Propagule size and predispersal damage by insects affect establishment and early growth of mangrove seedlings. Oecologia 135, 564–575.

Sousa, W.P., Kennedy, P.G., Mitchell, B.J., Ordóñez, B.M., 2007. Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? Ecol. Monogr. 77, 53–76.

Sousa, W.P., Mitchell, B.J., 1999. The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos 86, 55–66.

Sousa, W.P., Quek, S.P., Mitchell, B.J., 2003b. Regeneration of *Rhizophora mangle* in a Caribbean mangrove forest: interacting effects of canopy disturbance and a stem-boring bettle. Oecologia 137, 436–445.

Sperry, J.S., Tyree, M.T., Donnelly, J.R., 1988. Vulnerability of xylem to embolism in a mangrove vs. an inland species of *Rhizophoraceae*. Physiol. Plant. 74, 276–283.

Stevens, P.W., Fox, S.L., Montague, C.L., 2006. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetlands Ecol. Manage. 14, 435–444.

Stuart, S.A., Choat, B., Martin, K.C., Holbrook, N.M., Ball, M.C., 2007. The role of freezing in setting the latitudinal limits of mangrove forests. New Phytol. 173, 576–583.

Suarez, N., Sobrado, M.A., 2000. Adjustments in leaf water relations of mangrove (*Avicennia germinans*) seedlings grown in a salinity gradient. Tree Physiol. 20, 277–282.

Thibodeau, F.R., Nickerson, N.H., 1986. Differential oxidation of mangrove substrate by *Avicennia germinans* and *Rhizophora mangle*. Am. J. Bot. 73, 512–516.

Tilman, D., 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol. Monogr. 57, 189–214.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Tuffers, A., Naidoo, G., von Willert, D.J., 2001. Low salinities adversely affect photosynthetic performance of the mangrove *Avicennia marina*. Wetlands Ecol. Manage. 9, 235–242.

Turnbull, M.H., Schmidt, S., Erskine, P.D., Richards, S., Stewart, G.R., 1996. Root adaptation and nitrogen source acquisition in natural ecosystems. Tree Physiol. 16, 941–948.

Twilley, R.R., 1995. Properties of mangrove ecosystems related to the energy signature of coastal environments. In: Hall, C.A.S. (Ed.), Maximum Power: The Ideas and Applications of H.T. Odum. University Press of Colorado, Niwot, pp. 43–62.

Twilley, R.R., 1998. Mangrove wetlands. In: Messina, M.G., Conner, W.H. (Eds.), Southern Forested Wetlands Ecology and Management. Lewis Publishers, Boca Raton, pp. 445–473.

Twilley, R.R., Rivera-Monroy, V.H., Chen, R., Botero, L., 1998. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. Mar. Pollut. Bull. 37, 404–419.

Ungar, I.A., 1982. Germination ecology of halophytes. In: Sen, D., Rajpurohit, K. (Eds.), Contributions to the Ecology of Halophytes. Tasks for vegetation science 2. Dr. W. Junk Publishers, The Hague, pp. 143–154.

Urban, O., 2003. Physiological impacts of elevated CO_2 concentration ranging from molecular to whole plant responses. Photosynthetica 41, 9–20.

Valiela, I., Bowen, J.L., York, J.K., 2001. Mangrove forests: one of the world's threatened major tropical environments. BioScience 51, 807–815.

van den Boogaard, R.S., Goubitz, S., Veneklass, E.J., Lambers, H., 1996. Carbon and nitrogen economy of four *Triticum aestivum* cultivars differing in relative growth rate and water use efficiency. Plant Cell Environ. 19, 998–1004.

von Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Wang, W.-Q., Wang, M., Lin, P., 2003. Seasonal changes in element contents in mangrove element retranslocation during leaf senescence. Plant Soil 252, 187–193.

Wang, W., Xiao, Y., Chen, L.Z., Lin, P., 2007. Leaf anatomical responses to periodical waterlogging in simulated semidiurnal tides in mangrove *Bruguiera gymnorrhiza* seedlings. Aquat. Bot. 86, 223–228.

Warren, J.H., Underwood, A.J., 1986. Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. J. Exp. Mar. Biol. Ecol. 102, 223–225.

Watson, J.G., 1928. Mangrove forests of the Malay Peninsula. Malayan Forest Rec. 6, 1–275.

Werner, A., Stelzer, R., 1990. Physiological responses of the mangrove *Rhizophora mangle* grown in the absence and presence of NaCl. Plant Cell Environ. 13, 243–255.

Whelan, K.R.T., 2005. The Successional Dynamics of Lightning-initiated Canopy Gaps in the Mangrove Forests of Shark River, Everglades National Park, USA, Florida International University, Miami.

Whelan, K.R.T., Smith III, T.J., Cahoon, D.R., Lynch, J.C., Anderson, G.H., 2005. Groundwater control of mangrove surface elevation: shrink and swell varies with soil depth. Estuaries 28, 833–843.

Woodroffe, C.D., 1990. The impact of sea-level rise on mangrove shorelines. Prog. Phys. Geogr. 14, 483–520.

Woodroffe, C.D., 1992. Mangrove sediments and geomorphology. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, pp. 7–41.

Woodroffe, C.D., 1999. Response of mangrove shorelines to sea-level change. Tropics 8, 159–177.

Yáñez-Espinosa, L., Terrazas, T., López-Mata, L., 2001. Effects of flooding on wood and bark anatomy of four species in a mangrove forest community. Trees Struct. Funct. 15, 91–97.

Yates, E.J., Ashwath, N., Midmore, D.J., 2002. Responses to nitrogen, phosphorus, potassium and sodium chloride by three mangrove species in pot culture. Trees Struct. Funct. 16, 120–125.

Ye, Y., Tam, N.F.-Y., Lu, C.-Y., Wong, Y.-S., 2005. Effects of salinity on germination, seedling growth and physiology of three salt-secreting mangrove species. Aquat. Bot. 83, 193–205.

Ye, Y., Tam, N.F.Y., Wong, Y.S., Lu, C.Y., 2003. Growth and physiological responses of two mangrove species (*Bruguiera gymnorrhiza* and *Kandelia candel*) to waterlogging. Environ. Exp. Bot. 49, 209–221.

Ye, Y., Tam, N.F.Y., Wong, Y.S., Lu, C.Y., 2004. Does sea level rise influence propagule establishment, early development and physiology of *Kandelia candel* and *Bruguiera gymnorrhiza*? J. Exp. Mar. Biol. Ecol. 306, 197–215.

Youssef, T., Saenger, P., 1996. Anatomical adaptive strategies to flooding and rhizophere oxidation in mangrove seedlings. Aust. J. Bot. 44, 297–313.

Youssef, T., Saenger, P., 1998. Photosynthetic gas exchange and accumulation of phytotoxins in mangrove seedlings in response to soil physico-chemical characteristics associated with waterlogging. Tree Physiol. 18, 317–324.

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Review

Allometry, biomass, and productivity of mangrove forests: A review

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Abstract

We review 72 published articles to elucidate characteristics of biomass allocation and productivity of mangrove forests and also introduce recent progress on the study of mangrove allometry to solve the site- and species-specific problems. This includes the testing of a common allometric equation, which may be applicable to mangroves worldwide. The biomass of mangrove forests varies with age, dominant species, and locality. In primary mangrove forests, the above-ground biomass tends to be relatively low near the sea and increases inland. On a global scale, mangrove forests in the tropics have much higher above-ground biomass than those in temperate areas. Mangroves often accumulate large amounts of biomass in their roots, and the above-ground biomass to below-ground biomass ratio of mangrove forests is significantly low compared to that of upland forests (ANCOVA, $P < 0.01$). Several studies have reported on the growth increment of biomass and litter production in mangrove forests. We introduce some recent studies using the so-called ‘‘summation method’’ and investigate the trends in net primary production (NPP). For crown heights below 10 m, the above-ground NPP of mangrove forests is significantly higher (ANOVA, $P < 0.01$) than in those of tropical upland forests. The above-ground litter production is generally high in mangrove forests. Moreover, in many mangrove forests, the rate of soil respiration is low, possibly because of anaerobic soil conditions. These trends in biomass allocation, NPP, and soil respiration will result in high net ecosystem production, making mangrove forests highly efficient carbon sinks in the tropics.

Keywords: Common allometric equation; Growth; Litter; Low T/R ratio; Net ecosystem production; Net primary production

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1. Introduction

Forests form a major component of the carbon reserves in the world’s ecosystems (Whittaker and Likens, 1975) and greatly influence the lives of other organisms as well as human societies. Tree biomass provides various benefits, including safe habitats, food, and timber (Nagelkerken et al., 2008; Walters et al., 2008). Mangrove trees are found along tropical and subtropical coasts and are the only known woody halophytes. A part of their productivity may flow into adjacent ecosystems, or conversely, they may receive organic materials from estuarine or oceanic ecosystems (Ong, 1993; Kristensen et al., 2008).

The field survey of mangrove biomass and productivity is rather difficult due to muddy soil conditions and the heavy weight of the wood. The peculiar tree form of mangroves, especially their unusual roots, has long attracted the attention of botanists and ecologists (Tomlinson, 1986). How can they stand upright in such soft and wet mud? This is a basic question that

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many researchers have asked about mangrove trees. Yet, a simple answer may lie in the root biomass. To maintain a bottom-heavy tree form (Ong et al., 2004) or a low ratio of top biomass to root biomass (*T*/*R* ratio; Komiyama et al., 2000), mangroves might allocate a great deal of biomass to their roots. This phenomenon may produce peculiar conditions for ecosystem processes in root zones owing to the anaerobic conditions.

Over the years, forest ecologists have developed various methods to estimate the biomass of forests. Three main methods have been developed for estimating forest biomass: the harvest method, the mean-tree method, and the allometric method. In a mature mangrove forest, the total weight of an individual tree often reaches several tons (Komiyama et al., 2005). Therefore, the harvest method cannot be easily used in mature forests and in itself is not reproducible because all trees must be destructively harvested. The mean-tree method is utilized only in forests with a homogeneous tree size distribution, such as plantations. The allometric method estimates the whole or partial weight of a tree from measurable tree dimensions, including trunk diameter and height, using allometric equations. This is a nondestructive method and is thus useful for estimating temporal changes in forest biomass by means of subsequent measurements. However, the site- and species-specific dependencies of allometric equations pose a problem to researchers because tree weight measurement in mangrove forests is labor-intensive.

Based on studies of forest biomass using the allometric method and other characters, Kira and Shidei (1967) summarized the so-called ''summation method'' for estimating the net primary production (NPP) of forests. In this method, the rates of growth increment, death, and consumption by herbivores, are summed to obtain the NPP. The gross primary production (GPP) of forests can then be calculated by adding the rate of metabolic respiration to the NPP.

Recently, interest has grown in the study of carbon fluxes of an entire ecosystem, which includes carbon emissions from soil respiration. Net ecosystem production (NEP) is a sophisticated criterion to judge carbon fixation from the NPP and the rate of soil respiration. One method for estimating the NEP is through the eddy covariance. Essentially, this consists of taking rapid measurements of the vertical component of air velocity and the concentration of carbon dioxide/water vapor in the air above forest canopies, and taking their covariance. However, this method requires large equipment in mangrove forests, high-priced instruments, and complex computation (Monji et al., 2002).

In this review, we discuss the present status of studies on allometric equations, trends in biomass allocation, and trends in productivity for both above-ground and below-ground parts of mangrove forests. We also show some examples of mangrove studies for estimating the NEP by using the summation method.

2. Recent progress of studies on mangrove allometry

In many organisms, the growth rate of one part of the organism is proportional to that of another. This is the basic theory of allometric relationships, and therefore, the trunk diameter of a tree is, for example, highly correlated with trunk weight. If a range of tree sizes is measured, a regression equation can be derived for predicting tree weight. Since tree diameter is easy to measure but tree weight is much more difficult to determine, this gives a relatively easy way to estimate the standing biomass of forest stands. However, allometric relationships often show site- or species-dependency (e.g., Clough et al., 1997; Smith and Whelan, 2006). Sampling of even 20 or 30 trees of the dominant species at each site to obtain allometric relationships is extremely tedious and not always practical, apart from being destructive.

Allometric equations for mangroves have been developed for several decades to estimate biomass and subsequent growth. Most studies have used allometric equations for single-stemmed trees, but mangroves sometimes have multi-stemmed tree forms, as often seen in *Rhizophora*, *Avicennia*, and *Excoecaria* species (Clough et al., 1997; Dahdouh Guebas and Koedam, 2006). Clough et al. (1997) showed that the allometric relationship can be used for trunks in a multi-stemmed tree. Moreover, for dwarf mangrove trees, allometric relationships have been used to estimate the biomass (Ross et al., 2001).

For studies on single-stemmed trees published from 1984 to 2000, Saenger (2002) cited 43 allometric equations on above-ground biomass. His review and subsequent studies by Tam et al. (1995), Ong et al. (2004), Comley and McGuinness (2005), and Soares and Schaeffer-Novelli (2005) provide a good overall survey of the relevant literature. They found that species-specific trait of allometry (i.e., the allometric equation) is significantly different among mangrove tree species. However, the question of whether the allometry of a particular mangrove species is site-specific remains contentious. Clough et al. (1997) found different relationships in different sites, although Ong et al. (2004) reported similar equations applied to two different sites for *Rhizophora apiculata*. This issue is important for practical uses of allometric equations. If the equations are segregated by species and site, then different equations have to be determined for each site (Table 1).

On both the species- and site-specific issues of allometry, Chave et al. (2005) and Komiyama et al. (2005) proposed the use of a common allometric equation for mangroves. The common allometric equation that Komiyama et al. (2005) proposed is based on the pipe model (Shinozaki et al., 1964) and the static model of plant form (Oohata and Shinozaki, 1979). These models predict that the partial weight of the trunk at a certain height physically sustains the weight of the upper tree body, regardless of tree species and locality.

By using these two theories, Komiyama et al. (2005) derived equations with trunk diameter and wood density as parameters, and found good fits with 104 sample trees comprising 10 mangrove species from Thailand and Indonesia (the data, Tamai et al., 1986; Komiyama et al., 1988, are included in this common equation).

The common equation of Chave et al. (2005) was established based on statistical analysis but nevertheless consisted of the same two parameters used by Komiyama et al. (2005) (see Table 1). These two common equations have the advantage of

Table 1
Allometric equations for various mangroves based on DBH (cm)

Above-ground tree weight (W_{top} in kg)	Below-ground tree weight (W_R in kg)
Avicennia germinans $W_{top} = 0.140\text{DBH}^{2.40}$ $r^2 = 0.97$, $n = 45$, $D_{max} = 4$ cm, Fromard et al. (1998)[a] $W_{top} = 0.0942\text{DBH}^{2.54}$ $r^2 = 0.99$, $n = 21$, D_{max}: unknown, Imbert and Rollet (1989)[a]	*Avicennia marina* $W_R = 1.28\text{DBH}^{1.17}$ $r^2 = 0.80$, $n = 14$, $D_{max} = 35$ cm, Comley and McGuinness (2005)
A. marina $W_{top} = 0.308\text{DBH}^{2.11}$ $r^2 = 0.97$, $n = 22$, $D_{max} = 35$ cm, Comley and McGuinness (2005)	*Bruguiera* spp. $W_R = 0.0188(D^2H)^{0.909}$ r^2: unknown, $n = 11$, $D_{max} = 33$ cm, Tamai et al. (1986) c.f., $H = D/(0.025D + 0.583)$
Laguncularia racemosa $W_{top} = 0.102\text{DBH}^{2.50}$ $r^2 = 0.97$, $n = 70$, $D_{max} = 10$ cm, Fromard et al. (1998)[a] $W_{top} = 0.209\text{DBH}^{2.24}$ $r^2 = 0.99$, $n = 17$, D_{max}: unknown, Imbert and Rollet (1989)[a]	*Bruguiera exaristata* $W_R = 0.302\text{DBH}^{2.15}$ $r^2 = 0.88$, $n = 9$, $D_{max} = 10$ cm, Comley and McGuinness (2005)
Rhizophora apiculata $W_{top} = 0.235\text{DBH}^{2.42}$ $r^2 = 0.98$, $n = 57$, $D_{max} = 28$ cm, Ong et al. (2004)	*Ceriops australis* $W_R = 0.159\text{DBH}^{1.95}$ $r^2 = 0.87$, $n = 9$, $D_{max} = 8$ cm, Comley and McGuinness (2005)
Rhizophora mangle $W_{top} = 0.178\text{DBH}^{2.47}$ $r^2 = 0.98$, $n = 17$, D_{max}: unknown, Imbert and Rollet (1989)[a]	*R. apiculata* $W_R = 0.00698\text{DBH}^{2.61}$ $r^2 = 0.99$, $n = 11$, $D_{max} = 28$ cm, Ong et al. (2004) c.f., $W_{stilt} = 0.0209\text{DBH}^{2.55}$ $r^2 = 0.84$, $n = 41$
Rhizophora spp. $W_{top} = 0.128\text{DBH}^{2.60}$ $r^2 = 0.92$, $n = 9$, $D_{max} = 32$ cm, Fromard et al. (1998)[a] $W_{top} = 0.105\text{DBH}^{2.68}$ $r^2 = 0.99$, $n = 23$, $D_{max} = 25$ cm, Clough and Scott (1989)[a]	*Rhizophora stylosa* $W_R = 0.261\text{DBH}^{1.86}$ $r^2 = 0.92$, $n = 5$, $D_{max} = 15$ cm, Comley and McGuinness (2005)
Bruguiera gymnorrhiza $W_{top} = 0.186\text{DBH}^{2.31}$ $r^2 = 0.99$, $n = 17$, $D_{max} = 25$ cm, Clough and Scott (1989)[a]	*Rhizophora* spp. $W_R = 0.00974(D^2H)^{1.05}$ r^2: unknown, $n = 16$, $D_{max} = 40$ cm, Tamai et al. (1986) c.f., $H = D/(0.02D + 0.678)$
Bruguiera parviflora $W_{top} = 0.168\text{DBH}^{2.42}$ $r^2 = 0.99$, $D_{max} = 25$ cm, $n = 16$, Clough and Scott (1989)[a]	*Xylocarpus granatum* $W_R = 0.145\text{DBH}^{2.55}$ $r^2 = 0.99$, $n = 6$, $D_{max} = 8$ cm, Poungparn et al. (2002)
Ceriops australis $W_{top} = 0.189\text{DBH}^{2.34}$ $r^2 = 0.99$, $n = 26$, $D_{max} = 20$ cm, Clough and Scott (1989)[a]	Common equation $W_R = 0.199p^{0.899}D^{2.22}$ $r^2 = 0.95$, $n = 26$, $D_{max} = 45$ cm, Komiyama et al. (2005)
Xylocarpus grnatum $W_{top} = 0.0823\text{DBH}^{2.59}$ $r^2 = 0.99$, $n = 15$, $D_{max} = 25$ cm, Clough and Scott (1989)[a]	
Common equation $W_{top} = 0.251pD^{2.46}$ $r^2 = 0.98$, $n = 104$, $D_{max} = 49$ cm, Komiyama et al. (2005) $W_{top} = 0.168p\text{DBH}^{2.47}$ $r^2 = 0.99$, $n = 84$, $D_{max} = 50$ cm, Chave et al. (2005)	

D_{stilt}: the weight of prop root of *R. apiculata*.

[a] After Saenger (2002), Table 8.3 on p. 260. D_{max}: the upper range of samples.

requiring only two parameters, even though Soares and Schaeffer-Novelli (2005) list a large number of parameters in their allometric equations for mangroves. The measurement of trunk diameter or girth is more practical than other parameters, especially for those working in closed and tall canopies where tree height is difficult to accurately measure. Wood density differs significantly in different mangrove species, but less for individuals within a species (Komiyama et al., 2005).

The common equation of Komiyama et al. (2005) for above-ground weight was compared with other equations (Fig. 1, Table 1) for preliminary checking of its applicability. The two lines on the graph show the common equations for *R. apiculata* (wood density = 0.770 g cm^{-3}) and *Avicennia alba* (wood density = 0.506 g cm^{-3}), representing a heavy and a light wood species, respectively. We calculated the relative error (RE) between common and respective site-specific equations from 10 cm to the maximum trunk diameter of used samples at intervals of 5 cm. The calculation of RE was performed with the following formula: $\text{RE} = (w_{top} - W_{top})/W_{top}$, where w_{top} is the above-ground weight estimated from site-specific equations and W_{top} is from the common equation.

For *Rhizophora* species, the relative error of the common equation was −9.84 to +10.3% for the site-specific equation of Clough and Scott (1989), −5.81 to −4.94% for that of Imbert and Rollet (1989), −8.44 to +6.79% for that of Fromard et al. (1998), and +6.81 to +10.8% for that of Ong et al. (2004). On *Avicennia* species, relative error was −11.7 to +3.99% for that of Fromard et al. (1998), −4.05 to −10.8% for that of Imbert and Rollet (1989), and −13.4 to −3.26% for that of Clough et al. (1997). Only the equation for *Avicennia* species of Comley and McGuinness (2005) had a high relative error, up to −30.1%, and their equation showed a remarkable difference from the common equation for large trunk diameter (Fig. 1).

The common equation estimated the above-ground weight of mangroves generally within a 10% RE compared to use of site-specific equations. This would imply that the allometric relationship of mangrove species does not differ greatly among sites for the same species, suggesting that wood density may be an important determinant. Thus, the allometric equation of mangrove species is considered to be highly species-specific but less site-specific. Comparing two common equations, the estimation of Chave et al. (2005) gave lower above-ground weight estimates than that of Komiyama et al. (2005) when the same wood density was used.

For total understanding of forest biomass, the allometric equations for root weight are essential. Unfortunately, only a few equations are available because complete extraction of

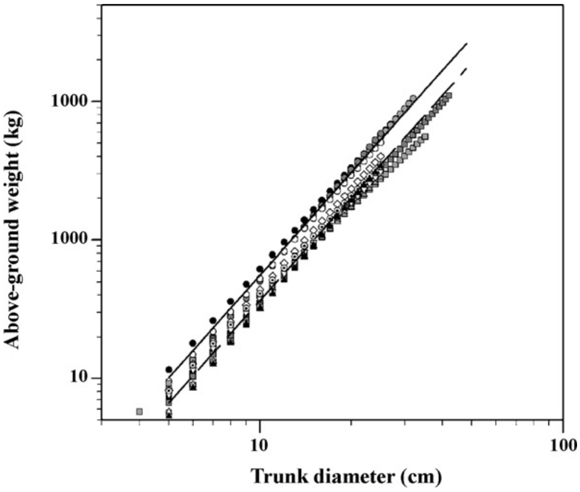

Fig. 1. Test of the common equation on the allometric relationship between trunk diameter and above-ground weight of a tree. Two lines show the relationship for *Rhizophora apiculata* (wood density = 0.770 g cm^{-3}, upper line) and *Avicennia alba* (wood density = 0.506 g cm^{-3}, lower line) based on the common equation (Komiyama et al., 2005). Dots on the graph show the results of estimation using site-specific equations from Ong et al. (2004) (●: *R. apiculata*), Fromard et al. (1998) (●: *Rhizophora* spp.; ■: *A. germinans*; △: *L. racemosa*), Clough and Scott (1989) (●: *Rhizophora* spp.; ▽: *B. gymnorrhiza*; ◇: *B. parviflora*; ⊕: *C. australis*; ▲: *X. grnatum*), Imbert and Rollet (1989) (○: *R. mangle*; □: *A. germinans*; ▲: *L. racemosa*;), Clough et al. (1997) (■: *A. marina*), Comley and McGuinness (2005) (■: *A. marina*).

roots from mangrove soils is a difficult and tedious process. Nevertheless, a few studies have published equations for estimating the root weight and have included a common equation (Table 1). We should note that different extraction methods were used in the different studies. Tamai et al. (1986) physically pulled out the roots of individual trees of *Rhizophora* and *Bruguiera* species. In soft mud substrates, loss with this method would mainly be in the fine-root fraction, unless large roots snap in the process of being pulled out. Komiyama et al. (2000) used the trench method for analyzing horizontal distribution of root density for *Ceriops tagal*. Ong et al. (2004) followed loosened individual roots into the mud using jets of water for *R. apiculata*, which resulted in minimal loss of recovered roots. Finally, in Comley and McGuinness (2005), a ‘‘root ball’’ within a 2 m radius and up to 1 m in depth around the sample tree, was mechanically excavated. With this method, the possibility exists of root contamination from neighboring trees. Thus, studies on the allometric relationship of mangrove roots are still needed due to the paucity of study cases as well as the differences in root extraction methods.

3. Trends in mangrove biomass

We examined data from 23 papers published in the past 50 years on the biomass of mangrove forests. Of these, only nine dealt with both above-ground and below-ground biomass (Table 2). The highest above-ground biomass, 460 t ha^{-1}, was found in a forest dominated by *R. apiculata* in Malaysia (Putz and Chan, 1986). Above-ground biomass of more than 300 t ha^{-1} was also reported in mangrove forests in Indonesia (Komiyama et al., 1988) and French Guiana (Fromard et al., 1998). The above-ground biomass was less than 100 t ha^{-1} in most secondary forests or concession areas. In high-latitude areas (>24° 23′N or S), primary forests mostly have an above-ground biomass of around 100 t ha^{-1}, however, even at 27° 24′ S, an above-ground biomass of 341 t ha^{-1} was reported for an *Avicennia marina* forest (Mackey, 1993). The lowest above-ground biomass reported was 7.9 t ha^{-1} for a *Rhizophora mangle* forest in Florida, USA (Lugo and Snedaker, 1974). The canopy height of mangrove forests is generally lower at higher latitudes (Pool et al., 1977; Saenger and Snedaker, 1993). Therefore, in low latitudes, primary or mature mangrove forests generally have high above-ground biomass. The above-ground biomass is always low in temperate areas and may be related to different climatic conditions, such as temperature, solar radiation, precipitation, and frequency of storms.

Mangrove forests usually show ‘‘zonation’’ patterns. In Southeast Asia, *Sonneratia* or *Avicennia* stands are often found on the sea front, and *Rhizophora* or *Bruguiera* stands are distributed more inland (e.g., Watson, 1929), although Ellison et al. (2000) questioned the concept of ‘‘zonation’’. In a primary mangrove forest on Halmahera Island in eastern Indonesia, Komiyama et al. (1988) estimated the above-ground biomass to be 169.1, 356.8, and 436.4 t ha^{-1} for *Sonneratia*, *Rhizophora*, and *Bruguiera* stands, respectively. Fromard et al. (1998) estimated the above-ground biomass to be 180.0 and 315.5 t ha^{-1}, respectively for *Avicennia* and *Rhizophora* stands in French Guiana. Based on these figures, the above-ground biomass tends to be relatively low in stands near the sea and increases inland. One possible explanation for this gradient may be that *Sonneratia* and *Avicennia* stands are usually found on newly deposited sediments as the pioneer stage in mangrove areas. Apart from the possible successional explanation, environmental factors such as soil properties and nutrient status may also affect the growth rate in mangrove biomass.

The pattern of biomass allocation to the above-ground organs of *Rhizophora* stands is shown in Fig. 2 (data source: Golley et al., 1962; Lugo and Snedaker, 1974; Aksornkoae, 1975; Christensen, 1978; Tamai et al., 1986; Komiyama et al., 1988; Kusmana et al., 1992; Ong et al., 1995). In all stands, stems and branches comprise the largest proportion of above-ground biomass. A tendency exists for the stem and branch portion to become larger as total above-ground biomass increases. The biomass of prop roots accounted for 15–17% of the above-ground biomass in mature stands. The prop roots formed a part of the root system of *Rhizophora* trees that was nearly equal to the branch biomass. Leaf biomass comprised the smallest portion of above-ground biomass and varied from 0.4 to 29.8 t ha^{-1}. In mature forests, the leaf/woody biomass ratio was quite low.

Previous below-ground biomass studies of mangrove forests are also listed in Table 2. In a primary mangrove area on Halmahera Island in eastern Indonesia, a large below-ground biomass was estimated at 196.1 t ha^{-1} in a *R. apiculata* stand. In this site, the below-ground biomass was 180.7 and 38.5 t ha^{-1} in a *Bruguiera gymnorrhiza* stand and a *Sonneratia alba* stand, respectively. These values included the prop roots,

Table 2
List of above-ground (ABG) and below-ground biomass (BGB) of worldwide mangrove forests

Region	Location	Condition or age	Species	ABG (t ha^{-1})	BGB (t ha^{-1})	H (m)	BA (m^2 ha^{-1})	Reference
Pacific and Australia								
Malaysia (Matang)	4°48′N, 100°35′E	>80	*R. apiculata* dominated forest	460.0	–	–	–	Putz and Chan (1986)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*B. gymnorrhiza* forest	436.4	180.7	22.4	35.9	Komiyama et al. (1988)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*B. gymnorrhiza* forest	406.6	110.8	26.4	36.2	Komiyama et al. (1988)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*R. apiculata* forest	356.8	196.1	21.2	25.1	Komiyama et al. (1988)
Australia	27°24′S, 153°8′E	Secondary forest	*A. marina* forest	341.0	121.0	16.4	–	Mackey (1993)
Thailand (Ranong Southern)	9°58′N, 98°38′E	Primary forest	*Rhizophora* spp. forest	298.5	272.9**	–	31.30	Komiyama et al. (1987)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*R. apiculata* forest	299.1	177.2	15.5	22.8	Komiyama et al. (1988)
Thailand (Ranong Southern)	9°N, 98°E	Primary forest	*Rhizophora* spp. forest	281.2	11.76	10.6	24.0	Tamai et al. (1986)
Thailand (Ranong Southern)	9°N, 98°E	Primary forest	*B. gymnorrhiza* forest	281.2*	106.3**	–	31.30	Komiyama et al. (1987)
Thailand (Ranong Southern)	9°N, 98°E	Primary forest	*Sonneratia* forest	281.2*	68.1**	–	31.30	Komiyama et al. (1987)
Indonesia (East Sumatra)	0°21′N, 103°48′E	Concession area	*B. sexangula* stand	279.0	–	21.7	22.1	Kusmana et al. (1992)
Malaysia (Matang)	4°48′N, 100°35′E	>80	*R. apiculata* dominated forest	270.0	–	–	–	Putz and Chan (1986)
Sri Lanka	8°15′N, 79°50′E	Fringe	*Rhizophora*	240	–	7.2	43.8	Amarasinghe and Balasubramaniam (1992)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*R. apiculata* forest	216.8	98.8	–	18.7	Komiyama et al. (1988)
India (Andaman Island)	12°N	Primary forest	*Rhizophora* forest	214.0	–	22.5	15.7	Mall et al. (1991)
Malaysia (Matang)	4°N	28-year-old	*R. apiculata* stand	211.8	–	15.0	–	Ong et al. (1982)
Sri Lanka	8°15′N, 79°50′E	Fringe	*Avicennia*	193.0	–	10.3	29.7	Amarasinghe and Balasubramaniam (1992)
Indonesia (East Sumatra)	0°21′N, 103°48′E	Concession area	*B. sexangula* stand	178.8	–	20.1	15.2	Kusmana et al. (1992)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*R. stylosa* forest	178.2	94.0	22.3	14.0	Komiyama et al. (1988)
Sri Lanka	8°15′N, 79°50′E	Fringe	Mixed forest	172.0	–	4.3	34.3	Amarasinghe and Balasubramaniam (1992)
Indonesia (Halmahera)	1°10′N, 127°57′E	Primary forest	*Sonneratia* forest	169.1	38.5	15.9	21.2	Komiyama et al. (1988)
Thailand (Phuket Southern)	8°N, 98°E	15-year-old	*R. apiculata* forest	159.0	–	8.0	–	Christensen (1978)
Australia	33°50′S, 151°9′E	Primary forest	*A. marina* forest	144.5	147.3	7.0	–	Briggs (1977)
Thailand (Trat Eastern)	12°12′N, 102°33′E	Secondary forest	Mixed forest	142.2	50.3	10.8	19.0	Poungparn (2003)
India (Andaman Island)	12°N	Primary forest	*Bruguiera* and *Ceriops* forest	124.0	–	12.5	6.0	Mall et al. (1991)
Australia	33°50′S, 151°9′E	Primary forest	*A. marina* forest	112.3	160.3	7.0	–	Briggs (1977)
Japan (Okinawa)	24°23′N, 124°08′E	Primary forest	*R. mucronata* forest	108.1	–	5.5	31.0	Suzuki and Tagawa (1983)
Japan (Okinawa)	24°23′N, 124°08′E	Primary forest	*B. gymnorrhiza* forest	97.6	–	5.5	32.9	Suzuki and Tagawa (1983)
Thailand (Satun Southern)	7°22′N, 100°03′E	Secondary forest	*C. tagal* forest	92.2	87.5	5.2	15.2	Komiyama et al. (2000)
Indonesia (East Sumatra)	0°21′N, 103°48′E	Concession area	*B. parviflora* stand	89.7	–	18.8	9.2	Kusmana et al. (1992)
Sri Lanka	8°15′N, 79°50′E	Riverine	Mixed forest	85.0	–	4.4	20.0	Amarasinghe and Balasubramaniam (1992)
Indonesia (East Sumatra)	0°21′N, 103°48′E	Concession area	*B. sexangula* stand	76.0	–	17.1	5.0	Kusmana et al. (1992)
Sri Lanka	8°15′N, 79°50′E	Island habitat	*Rhizophora*	71.0	–	3.9	11.4	Amarasinghe and Balasubramaniam (1992)
Thailand (Southern Pang-nga)	8°15′N, 79°50′E	Secondary forest	Mixed forest	62.2	28.0	6.5	11.4	Poungparn (2003)
Sri Lanka	8°15′N, 79°50′E	Riverine	Mixed forest	57.0	–	4.5	13.1	Amarasinghe and Balasubramaniam (1992)
Indonesia (East Sumatra)	0°21′N, 103°48′E	Concession area	*B. parviflora* stand	42.9	–	19.5	4.0	Kusmana et al. (1992)
Indonesia (East Sumatra)	0°21′N, 103°48′E	Concession area	*R. apiculata* stand	40.7	–	29.5	2.5	Kusmana et al. (1992)
Atlantic and Africa								

French Guiana	4°52′N, 52°19′E	Matured coastal	*Laguncularia*, *Avicennia*, *Rhizophora*	315.0	–	22.7	33.60	Fromard et al. (1998)
Panama	9°N	Primary forest	*Rhizophora* forest	279.2	306.2	–	–	Golley et al. (1975)
Kenya	4°25′S, 39°30′E	Primary forest	*R. mucronata* forest	249.0	–	12.0	–	Slim et al. (1996)
Dominican Republic	19°10′N, 64°40′E	50 years	*R. mangle*, *Laguncularia*, *A. germim*	233.0	–	–	26.80	Sherman et al. (2003)
French Guiana	5°30′N, 53°10′E	Matured riverine	*Laguncularia*, *Avicennia*	188.6	–	23.0	24.00	Fromard et al. (1998)
French Guiana	5°23′N, 52°50′E	Matured coastal	*Laguncularia*, *Avicennia*, *Rhizophora*	180.0	–	19.6	24.60	Fromard et al. (1998)
French Guiana	5°23′N, 52°50′E	Senescent forest	*Rhizophora*, *Avicennia*	143.3	–	–	18.50	Fromard et al. (1998)
French Guiana	5°23′N, 52°50′E	Matured riverine	*Rhizophora*, *Avicennia*	122.2	–	19.1	17.80	Fromard et al. (1998)
South Africa	29°48′S, 31°03′E	–	*B. gymnorrhiza*, *A. marina*	94.5	–	6.0	–	Steinke et al. (1995)
French Guiana	4°52′N, 52°19′E	Young stage	*Laguncularia*	71.8	–	7.7	20.60	Fromard et al. (1998)
Puerto-rico	18°N, 67°E	–	*R. mangle*	62.9	64.4	7.5	–	Golley et al. (1962)
USA (Florida)	25°27′N, 80°20′E	–	*R. mangle* and *A. germinas fringe*	56.0	–	4.0	13.54	Ross et al. (2001)
Kenya	4°25′S, 39°30′E	Primary forest	*C. tagal* forest	40.1	–	3.0	–	Slim et al. (1996)
French Guiana	5°23′N, 52°50′E	Pioneer stage 1 year	*Avicennia*	35.1	–	2.8	12.50	Fromard et al. (1998)
French Guiana	4°52′N, 52°19′E	Pioneer stage	*Laguncularia*	31.5	–	3.5	13.70	Fromard et al. (1998)
USA (Florida)	25°10′N, 80°45′E	–	*R. mangle* stand	12.5	–	1.2	–	Coronado-Molina et al. (2004)
USA (Florida)	26°N	–	*R. mangle* stand	7.9	–	–	–	Lugo and Snedaker (1974)

Remark: *ABG reported by Tamai et al. (1986). **Fine-root fraction was excluded from the BGB.

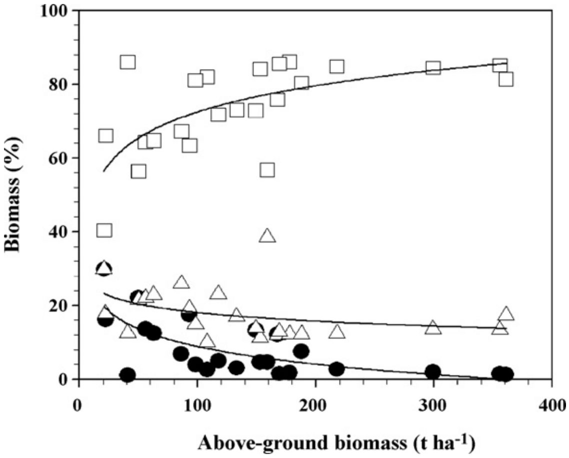

Fig. 2. Above-ground biomass allocation to each organ of *Rhizophora* trees. Closed circles indicate leaf biomass, triangles denote prop root biomass, and squares represent stem and branch biomass. Lines show the tendency for allocation. Data sources: Golley et al. (1962); Lugo and Snedaker (1974); Aksornkoae (1975); Christensen (1978); Tamai et al. (1986); Komiyama et al. (1988); Kusmana et al. (1992); Ong et al. (1995).

buttresses, pneumatophores, and fine-roots (<2 mm diameter; biomass varied from 6.1 to 9.1 t ha^{-1}; Komiyama et al., 1988).

Cairns et al. (1997) reviewed root biomass studies conducted worldwide in upland forests, finding that root biomass is normally below 150 t ha^{-1}. In mangrove forests, the root biomass is higher, which could be an adaptation for living on soft sediments. Mangroves may be unable to mechanically support their above-ground weight without a heavy root system. In addition, soil moisture may cause increased allocation of biomass to the roots (e.g., Kramer and Kozlowski, 1979), with enhanced cambial activity induced by ethylene production under submerged conditions (Yamamoto et al., 1995).

In Fig. 3, the relationship between above-ground and below-ground biomass of 12 mangrove stands (Tamai et al., 1986; Komiyama et al., 1988, 2000; Mackey, 1993; Poungparn, 2003) is compared to that of 91 upland forests (data from DeAngelis

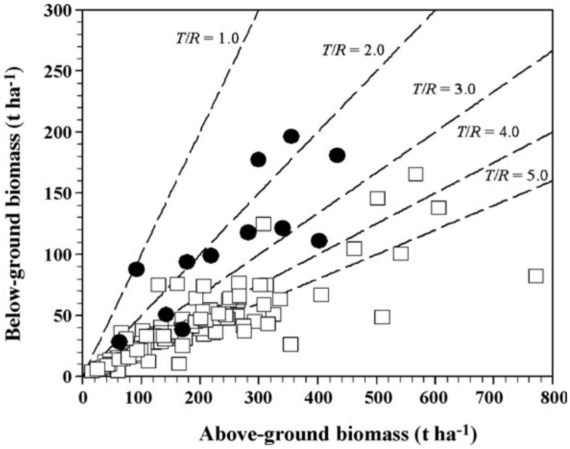

Fig. 3. The relationship between above-ground biomass and below-ground biomass. Closed circles represent mangrove forests, and squares denote upland forests. Broken lines indicate ranges of T/R = 1.0–5.0. Data sources: DeAngelis et al. (1981); Tamai et al. (1986); Komiyama et al. (1988); Mackey (1993); Komiyama et al. (2000); Poungparn (2003).

et al., 1981). The above-ground biomass consists of stem, branch, and leaf biomass, and the below-ground biomass consists of prop roots and below-ground root biomass. The above-ground biomass to below-ground biomass (*T*/*R*) ratio of mangrove forests was significantly lower than that of upland forests (ANCOVA, $P < 0.01$). The *T*/*R* ratio of mangrove forests varied between 1.1 (a *C. tagal* stand in Thailand) and 4.4 (a *Sonneratia* stand in Indonesia), and generally was between 2.0 and 3.0. In upland forests with above-ground biomass less than 300 t ha^{-1}, Cairns et al. (1997) found *T*/*R* ratios between 3.96 and 4.52. Thus, in mangrove forests, a large amount of biomass tends to be allocated to the root system.

4. Trends in mangrove productivity

In the summation method (Kira and Shidei, 1967), the net primary production, NPP, consists of three components (Fig. 4). From temporal changes in forest biomass estimated by the allometric method, the growth increment (*Y*) is obtained. The death, including above- and below-ground litter production (*L*), and the rate of grazing by herbivores (*G*) are the other two components. Then, the NPP, which is the gain in organic carbon used for the formation of plant tissues, is estimated from the rates of ($Y + L + G$). The net ecosystem production, NEP, can also be calculated by using the summation method (Fig. 4). The NEP includes the rate of respiration (R_h) produced by micro- and macro-organisms in the soil, and is calculated from the following formula: $\text{NEP} = \text{GPP} - (R_m + R_h) = \text{NPP} - R_h$. Using the above derivation, it becomes possible to estimate

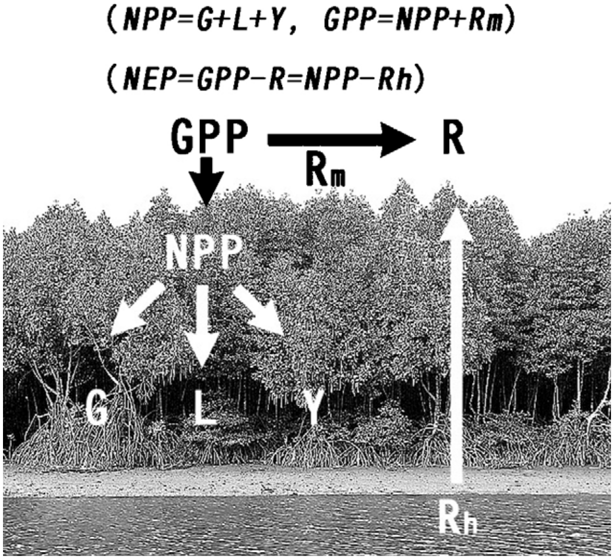

Fig. 4. The summation method used to calculate the net primary production (NPP) and the net ecosystem production (NEP) of forests. See main text for abbreviations.

Table 3
Net primary production (NPP) of the above-ground part and canopy height (*H*) of worldwide mangrove forests

Type	*H* (m) =	Latitude (°)	*Y* (t ha^{-1} yr^{-1})	*L* (t ha^{-1} yr^{-1})	NPP (t ha^{-1} yr^{-1})	Country	References
Rhizophora	3.5	8.15	6.77	6.24	13.01	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
Rhizophora + *Avicennia*	3.5	8.15	5.62	5.52	11.14	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
Rhizophora	3.5	8.15	4.33	4.41	8.74	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
Avicennia	3.5	8.15	1.40	3.74	5.14	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
Rhizophora + *Bruguiera*	30	8.30	–	–	19.50	PNG	Robertson et al. (1991)
Avicennia + *Sonneratia*	30	8.30	–	–	13.88	PNG	Robertson et al. (1991)
Rhizophora	7	25.27	–	–	12.10	Florida	Ross et al. (2001)
Rhizophora	0.5	25.27	–	–	8.10	Florida	Ross et al. (2001)
Rhizophora + *Avicennia*	6	18.40	1.99	4.96	6.95	Mexico	Day et al. (1996)
Avicennia	4	18.40	0.92	3.07	3.99	Mexico	Day et al. (1996)
Avicennia	6	18.40	2.02	4.10	6.12	Mexico	Day et al. (1996)
Rhizophora	11	8.00	20.00	6.70	26.70	Thailand	Christensen (1978)
Rhizophora	21	4.50	12.38	11.26	23.64	Malaysia	Ong et al. (1995)
Rhizophra	8.6	18.00	3.07	9.49	12.56	Puerto Rico	Golley et al. (1962)
Avicennia	20	18.40	12.06	12.52	24.58	Mexico	Day et al. (1987)
Rhizophora	6	18.40	7.72	8.35	16.07	Mexico	Day et al. (1987)
Rhizophora + *Lagunchularia* + *Avicennia*	24	19.10	–	–	16.80	Dominica	Sherman et al. (2003)
Rhizophora + *Lagunchularia* + *Avicennia*	24	19.10	–	–	23.60	Dominica	Sherman et al. (2003)
Rhizophora	7.2	7.50	–	–	22.90	Indonesia	Sukardjo and Yamada (1992)
Rhizophora	31.5	5.00	–	–	17.70	Malaysia	Putz and Chan (1986)

The growth increment (*Y*) and litter production (*L*) were used in the summation method for NPP using 12 studies, while other eight studies used different methods including the photosynthetic and the light absorption methods.

the NEP without determining total plant respiration (R_m), which is difficult to measure.

Several studies in the past couple of decades have examined the above-ground NPP of mangrove forests (Table 3). Eleven studies used the growth increment (Y) and litter production (L) of above-ground parts for calculating the NPP, and other eight studies used other methods, including the method using the light absorption of a canopy (Robertson et al., 1991) and using leaf turnover rates (Ross et al., 2001). The above-ground NPP ranged from a low of 3.99 t ha^{-1} yr^{-1} in an *Avicennia germinans* dominated stand in Mexico (Day et al., 1996) to a surprisingly high value of 26.70 t ha^{-1} yr^{-1} in a *R. apiculata* stand in southern Thailand (Christensen, 1978). For crown heights (H) less than 10 m, ten studies with values of Y and L (Table 3) gave the mean NPP as 9.30 t ha^{-1} yr^{-1}, which is significantly higher (ANOVA, $P < 0.01$) than the NPP of tropical upland forests reported by DeAngelis et al. (1981). In a recent review on the NPP of tropical forests, Clark et al. (2001) found that the above-ground NPP was mostly less than 10 t ha^{-1} yr^{-1} and the maximum 14.3 t ha^{-1} yr^{-1} among 39 stands. In the range of $H > 10$ m, Day et al. (1987) and Christensen (1978) estimated a high NPP. Some other NPP estimates using different methods gave high values, but these cannot be compared directly to estimates from the summation method.

Hence, the above-ground NPP of mangrove forests tends to be high compared to tropical upland forests, at least in the range of $H < 10$ m. The high NPP of mangrove forests may be partly due to their high litter production rates. Saenger and Snedaker (1993) collected litter production data from 91 mangrove forests worldwide and found a significant linear relationship between latitude and litter production. Using this relationship, they compared mangrove litter production to the litter production in other tropical and subtropical forests (Procter, 1984) and concluded that mangrove forests had 16% higher litter production than other equatorial forests. As for the growth increment of forest biomass, only 11 reports are currently available for mangroves (Table 3) and the growth increment varies widely, from 0.92 to 20.0 t ha^{-1} yr^{-1}.

We must refer to two aspects of the above NPP estimates. First, the rate of grazing by herbivores (G) was not included in the summation (Table 3) due to the paucity of studies describing herbivory on mangroves (Johnstone, 1981). However, it may be generally argued that herbivory is not important in mangroves because of their high tannin content. Second, while several studies have reported on the above-ground litter production in mangrove forests, few have examined the below-ground litter production. The rate of below-ground litter, especially fine-root litter, is underestimated in the above NPP estimates. The litter production of roots is very difficult to study and therefore poses a major obstacle in obtaining a total understanding of mangrove NPP. For future studies, it is necessary to enhance mangrove research on growth increment, the consumption by herbivores, and below-ground productivity.

To estimate the NEP, the magnitude of R_h from micro- and macro-organisms in the soil must also be estimated (Fig. 4). A major problem here is how to separate R_h from root respiration in the soil. Most mangroves develop peculiar root systems in which the aerenchyma tissues of below-ground roots are connected with lenticels on pneumatophores, prop roots, and buttresses above the ground (e.g., Tomlinson, 1986). Most metabolic respiration (R_m) from roots is considered to be released through the lenticels. In a recent experiment in an *A. alba* forest at Trat, eastern Thailand, the surface area of pneumatophores was closely related to the magnitude of root respiration (Aki Tanaka et al., Gifu University, personal communication). Therefore, below-ground roots of mangroves may make a small contribution to the soil respiration when soil respiration chambers are placed so as to avoid peumatophores.

The magnitude of soil respiration in sediments in terms of CO_2 flux has been studied in *Rhizophora* and *Avicennia* forests in Australia (Alongi et al., 2000; 0.18–5.56 t C ha^{-1} yr^{-1}) and southern Thailand (Alongi et al., 2001; 0.73–2.31 t C ha^{-1} yr^{-1}). Kristensen et al. (1995) found that the magnitude of CO_2 release from sediments was higher under submerged conditions than under exposed conditions. In a *Rhizophora* stand, soil respiration was estimated to be 2.28 t C ha^{-1} yr^{-1} (Kristensen et al., 1995). These studies suggest that CO_2 release from mangrove sediments is low, normally less than 3.0 t C ha^{-1} yr^{-1}. However, high soil respiration rates (11.61–20.41 t C ha^{-1} yr^{-1}) were reported by Mall et al. (1991) in mangrove forests on the Andaman Islands. In tropical rain forests, the magnitude of soil respiration normally ranges from 15.0 to 37.5 t C ha^{-1} yr^{-1} (Yoda, 1971). Little CH_4 flux has been detected in mangrove sediments (Alongi et al., 1999, 2000; Mukhopadhyay et al., 2002; Ohmori, 2002).

From the generally high NPP and low soil respiration as cited in the above studies, one may suppose that mangrove forests play an important role in the sequestration of atmospheric carbon dioxide. However, few studies have measured the biomass growth increment, litter production, and soil respiration concurrently within a mangrove stand. We show two preliminary studies on the NEP of mangrove forests.

For the above-ground portion of a *R. mangle* forest (crown height = 8.6 m) in Puerto Rico, Golley et al. (1962) estimated the above-ground biomass growth increment to be 3.07 t ha^{-1} yr^{-1} and litter production to be 9.49 t ha^{-1} yr^{-1}. They used an infrared CO_2 analyzer and estimated soil respiration rates to be 0.73 and 0.61 t C ha^{-1} yr^{-1} under submerged and exposed conditions, respectively. Assuming that half the day is spent submerged and the carbon content in plant bodies is 50%, the NEP is calculated to be 5.61 t C ha^{-1} yr^{-1}. This study is a pioneer work on the carbon fixation process of mangrove forests but done in a short period in May.

In a mangrove forest in eastern Thailand dominated by *R. apiculata*, *A. alba*, and *Xylocarpus granatum* (crown height = 17 m), Komiyama (2006) estimated the biomass growth increment including that of roots to be 11.02 t ha^{-1} yr^{-1}, above-ground litter production to be 10.49 t ha^{-1}yr^{-1}, and mean soil respiration (estimated with a CO_2 analyzer) to be 2.24 t C ha^{-1} yr^{-1}. In this mangrove forest, the NEP was calculated up to 8.52 t C ha^{-1} yr^{-1}. According to Pregitzer and

Euskirchen (2004), NEP estimates vary with forest age and are high in 30- to 120-year-old stands. They showed that the mean NEP of temperate forests was less than 4.5 t C $\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$ and may even be negative (-1.9 t C $\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$) in 0- to 10-year-old stands.

These results suggest that mangrove forests are highly efficient carbon sinks in the tropics. However, future studies should cover detailed examination on each component of carbon fluxes, especially the dynamics of the below-ground fraction including fine-roots. Mangroves live under extremely wet conditions and require a bottom-heavy tree form. Relatively high primary production and low decomposition processes in mangrove soils are considered to bring about unusual carbon dynamics.

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References

Aksornkoae, S., 1975. Structure, regeneration and productivity of mangroves in Thailand. Ph.D. Dissertation, Michigan University, 109 pp.

Alongi, D.M., Tirendi, F., Trott, L.A., 1999. Rate and pathways of benthic mineralization in extensive shrimp ponds of the Mekong Delta, Vietnam. Aquaculture 175, 269–292.

Alongi, D.M., Tirendi, F., Clough, B.F., 2000. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. Aquat. Bot. 68, 97–122.

Alongi, D.M., Wattayakorn, G., Pfitzner, J., Tirendi, F., Zagorskis, I., Brunskill, G.J., Davidson, A., Clough, B.F., 2001. Organic carbon accumulation and metabolic pathways in sediments of mangrove forests in southern Thailand. Mar. Geol. 179, 85–103.

Amarasinghe, M.D., Balasubramaniam, S., 1992. Net primary productivity of two mangrove forest stands on the northwest coast of Sri Lanka. Hydrobiologia 247, 37–47.

Briggs, S.V., 1977. Estimates of biomass in a temperate mangrove community. Aust. J. Ecol. 2, 369–373.

Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. Oecologia 111, 1–11.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99.

Christensen, B., 1978. Biomass and productivity of *Rhizophora apiculata* B1 in a mangrove in southern Thailand. Aquat. Bot. 4, 43–52.

Clark, D.A., Brown, S., Kicklighter, W., Chambers, J.Q., Thomlinson, J.R., Ni, J., Holland, E.A., 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol. Appl. 11, 371–374.

Clough, B.F., Scott, K., 1989. Allometric relationships for estimating above-ground biomass in six mangrove species. Forest Ecol. Manage. 27, 117–127.

Clough, B.F., Dixon, P., Dalhaus, O., 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. Aust. J. Bot. 45, 1023–1031.

Coronado-Molina, C., Day, J.W., Reyes, E., Prez, B.C., 2004. Standing crop and aboveground partitioning of a dwarf mangrove forest in Taylor River Slough, Florida. Wetlands Ecol. Manage. 12, 157–164.

Comley, B.W.T., McGuinness, K.A., 2005. Above- and below-ground biomass, and allometry of four common northern Australian mangroves. Aust. J. Bot. 53, 431–436.

Dahdouh Guebas, F., Koedam, N., 2006. Empirical estimate of the reliability of the use of the Point-Centered Quarter Method (PCQM): solutions to ambiguous field situations and description of the PCQM + protocol. Forest Ecol. Manage. 228, 1–18.

Day, J.W., Conner, W.H., Ley, L.F., Day, R.H., Navarro, A.M., 1987. The productivity and composition of mangrove forests, Laguna de Terminons, Mexico. Aquat. Bot. 27, 267–284.

Day, J.W., Coronado-molina, C., Vera-Herrera, F.R., Twilley, R., Rivera-Monroy, V.H., Alvarez-Guillen, H., Day, R., Conner, W., 1996. A 7-year record of above-ground net primary production in a southeastern Mexican mangrove forest. Aquat. Bot. 55, 39–60.

DeAngelis, D.L., Gardner, R.H., Shugart, H.H., 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Reichle, D.E. (Ed.), Dynamic Properties of Forest Ecosystems. International Biological Programme, vol. 23. Cambridge University Press, Cambridge, pp. 567–672.

Ellison, A.E., Mukherjee, B.B., Karim, A., 2000. Testing patterns of zonation in mangroves: scale dependence and environmental correlates in the Sundarbans of Bangladesh. J. Ecol. 88, 813–824.

Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J.L., Cadamuro, L., 1998. Structure above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115, 39–53.

Golley, F., Odum, H.T., Wilson, R., 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. Ecology 43, 9–19.

Golley, F.B., Mcginnis, J.T., Clements, R.G., Child, G.I., Duever, M.J., 1975. Mineral Cycling in a Tropical Moist Forest Ecosystem. Georgia Univ. Press, Athens.

Imbert, D., Rollet, B., 1989. Phytmassaerienne et production primaire dans la mangrove du Grand Cul-de-sac Marine (Guadeloupe, Antilles francaises). Bull. Ecol. 20, 27–39.

Johnstone, I.M., 1981. Consumption of leaves by herbivores in mixed mangrove stands. Biotropica 13, 252–259.

Kira, T., Shidei, T., 1967. Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. Jpn. J. Ecol. 17, 70–87.

Komiyama, A., 2006. What is required for scientists towards the mangrove management? In: Kyoto Symposium on Mangrove Management. pp. 1–17.

Komiyama, A., Ogino, K., Aksornkoae, S., Sabhasri, S., 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. J. Trop. Ecol. 3, 97–108.

Komiyama, A., Moriya, H., Prawiroatmodjo, S., Toma, T., Ogino, K., 1988. Forest primary productivity. In: Ogino, K., Chihara, M. (Eds.), Biological System of Mangrove. Ehime University, pp. 97–117.

Komiyama, A., Havanond, S., Srisawatt, W., Mochida, Y., Fujimoto, K., Ohnishi, T., Ishihara, S., Miyagi, T., 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) C. B. Rob.) forest. Forest Ecol. Manage. 139, 127–134.

Komiyama, A., Poungparn, S., Kato, S., 2005. Common allometric equations for estimating the tree weight of mangroves. J. Trop. Ecol. 21, 471–477.

Kramer, P.J., Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic Press, New York, 811 pp.

Kristensen, E., Holmer, M., Banta, G.T., Jensen, M.H., Hansen, K., 1995. Carbon nitrogen and sulfur cycling in sediments of the Ao Nam Bor mangrove forest, Phuket, Thailand: a review. Phuket Mar. Biol. Cent. Res. Bull. 60, 37–64.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Kusmana, C., Sabiham, S., Abe, K., Watanabe, H., 1992. An estimation of above ground tree biomass of a mangrove forest in east Sumatra, Indonesia. Tropics 1, 243–257.

Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Ann. Rev. Ecol. Syst. 5, 39–64.

Mackey, A.P., 1993. Biomass of the mangrove *Avicennia marina* (Forsk.) Vierh. near Brisbane, south eastern Queensland. Aust. J. Mar. Freshwater Res. 44, 721–725.

Mall, L.P., Singh, V.P., Garge, A., 1991. Study of biomass, litter fall, litter decomposition and soil respiration in monogeneric mangrove and mixed mangrove forests of Andaman Islands. Trop. Ecol. 32, 144–152.

Monji, N., Hamotani, K., Tosa, R., Fukagawa, T., Yabuki, K., Hirano, T., Jintana, V., Piriyayota, S., Nishimiya, A., Iwasaki, M., 2002. CO_2 and water vapor flux evaluations by modified gradient methods over a mangrove forest. J. Agric. Meteorol. 58, 63–69.

Mukhopadhyay, S.K., Biswas, H., De, T.K., Sen, B.K., Sen, S., Jana, T.K., 2002. Impact of Sundarban mangrove biosphere on the carbon dioxide and methane mixing ratios at the NE coast of Bay of Bengal. Indian Atmos. Environ. 36, 629–638.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Ohmori, K., 2002. Greenhouse gas flux from sediment enhanced by bioturbation. Nippon Suisan Gakkaishi 68, 740–741 (in Japanese).

Ong, J.E., 1993. Mangroves—a carbon source and sink. Chemosphere 27, 1097–1107.

Ong, J.E., Gong, W.K., Wong, C.H., 1982. Studies on Nutrient Levels in Standing Biomass, Litter and Slash in a Mangrove Forest. BIOTROP, Bogor, p. 44.

Ong, J.E., Gong, W.K., Clough, B.F., 1995. Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* B1 mangrove forests. J. Biogeogr. 22, 417–427.

Ong, J.E., Gong, W.K., Wong, C.H., 2004. Allometry and partitioning of the mangrove, *Rhizophora apiculata*. Forest Ecol. Manage. 188, 395–408.

Oohata, S., Shinozaki, K., 1979. A statistical model of plant form—further analysis of the pipe model theory. Jpn. J. Ecol. 29, 323–335.

Pool, D.J., Lugo, A.E., Snedaker, S.C., 1977. Litter production in mangrove forests of southern Florida and Puerto Rico. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 2. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, pp. 213–237.

Poungparn, S., 2003. Common allometric relationships for estimating the biomass of mangrove forests. Ph.D. dissertation, Gifu University, 87 pp.

Poungparn, S., Komiyama, A., Jintana, V., Piriyayaota, S., Sangtiean, T., Tanapermpool, P., Patanaponpaiboon, P., Kato, S., 2002. A quantitative analysis on the root system of a mangrove, *Xylocarpus granatum* Koenig. Tropics 12, 35–42.

Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Change Biol. 10, 2052–2077.

Procter, J., 1984. Tropical forest litterfall. II. The data set. In: Chadwick, A.C., Sutton, S.L. (Eds.), Tropical Rain Forest: Ecology and Management, Supplementary Volume. Blackwell Scientific Publications, Oxford, pp. 83–113.

Putz, F., Chan, H.T., 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. Forest Ecol. Manage. 17, 211–230.

Robertson, A.I., Daniel, P.A., Dixon, P., 1991. Mangrove forest structure and productivity in the Fly River estuary, Papua New Guinea. Mar. Biol. 111, 147–155.

Ross, M.S., Ruiz, P.L., Telesnicki, G.J., Meeder, J.F., 2001. Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (USA). Wetlands Ecol. Manage. 9, 27–37.

Saenger, P., 2002. Mangrove Ecology, Silviculture and Conservation. Kluwer Academic Press, The Netherlands, 360 pp.

Saenger, P., Snedaker, S.C., 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. Oecologia 96, 293–299.

Sherman, R.E., Fahey, T.J., Martinez, P., 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. Ecosystems 6, 384–398.

Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964. A quantitative analysis of plant form—the pipe model theory. II. Further evidence of the theory and its application in forest ecology. Jpn. J. Ecol. 14, 133–139.

Slim, F.J., Gwada, P.M., Kodjo, M., Hemminga, M.A., 1996. Biomass and litterfall of *Ceriops tagal* and *Rhizophora mucronata* in the mangrove forest of Gazi Bay, Kenya. Mar. Freshwater Res. 47, 999–1007.

Smith III, T.J., Whelan, K.R.T., 2006. Development of allometric relations for three mangrove species in South Florida for use in the Greater Everglades Ecosystem restoration. Wetland Ecol. Manage. 14, 409–419.

Soares, M.L.G., Schaeffer-Novelli, Y., 2005. Above-ground biomass of mangrove species. I. Analysis of models. East. Coast Shelf Sci. 65, 1–18.

Steinke, T.D., Ward, C.J., Rajh, A., 1995. Forest structure and biomass of mangroves in the Mgeni estuary, South Africa. Hydrobiologia 295, 159–166.

Sukardjo, S., Yamada, I., 1992. Biomass and productivity of a *Rhizophora mucronata* Lamarck plantation in Tritih, Central Java, Indonesia. Forest Ecol. Manage. 49, 195–209.

Suzuki, E., Tagawa, E., 1983. Biomass of a mangrove forest and a sedge marsh on Ishigaki Island, south Japan. Jpn. J. Ecol. 33, 231–234.

Tam, N.F.Y., Wong, Y.S., Lan, C.Y., Chen, G.Z., 1995. Community structure and standing crop biomass of a mangrove forest in Futian Nature Reserve, Shenzhen, China. Hydrobiologia 295, 193–201.

Tamai, S., Nakasuga, T., Tabuchi, R., Ogino, K., 1986. Standing biomass of mangrove forests in southern Thailand. J. Jpn. Forest Soc. 68, 384–388.

Tomlinson, P.B., 1986. The Botany of Mangrove. Cambridge University Press, Cambridge, pp. 419.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobilogy, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Watson, J.G., 1929. Mangrove Forest of the Malay Peninsula. Malay. For. Rec. No. 6. Fraser and Neave, Singapore, 276 pp.

Whittaker, R.H., Likens, G.E., 1975. The biosphere and man. In: Lieth, H., Whittaker, R.H. (Eds.), Primary Productivity of the Biosphere. Ecological Studies, vol. 14. Springer, Berlin, pp. 305–328.

Yamamoto, F., Sakata, T., Terazawa, K., 1995. Physiological, morphological and anatomical responses of *Fraxinus mandshurica* seedlings to flooding. Tree Physiol. 15, 713–719.

Yoda, K., 1971. Forest Ecology. Tsukiji Printing K.K., Tokyo, 331 pp. (in Japanese).

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Review

Molecular ecology and biogeography of mangrove trees towards conceptual insights on gene flow and barriers: A review

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Abstract

In this review the most recent contributions to the field of molecular ecology and biogeography of mangrove trees are considered. Emphasis is on the obtained information of the different molecular marker methods used in mangrove genetics and on the potential to infer biogeographical patterns. Isozymes on average showed low or even no polymorphism in mangrove trees similar as known in seagrasses. The outcrossing *Avicennia* seems to be the most variable mangrove tree for isozymes. Both low amounts of interpretable allozymes and difficulties in maintaining the enzyme activity have reduced the number of successful studies during the isozyme era. Dominant marker methods (RAPD, AFLP and ISSR) were successful to demonstrate differences in amplified DNA products at large-scale geographical distances within *Avicennia* species and to estimate species relationships. Hybrid testing seldom revealed hybridization among tree species. The most promising markers (microsatellites or SSR) were only recently developed and will continue to provide evidence in future studies. SSR loci in *Avicennia* seem to show relatively low levels of polymorphism, though clearly demonstrating that populations located at the edge of the species range can be even more depauperated. Populations located more central in their native range and situated along the same coastline such as reported in *Rhizophora*, are expected to be only weakly differentiated due to increased levels of gene flow. Haplotypic chloroplast variants (PCR-RFLP) or sequences revealed strong genetic structuring between populations of *Avicennia*, *Kandelia* and *Ceriops* from different biogeographical oceanic regions. Recent views on long-distance dispersal and on gene flow across oceans as well as along the same coastline are discussed. A comparative analysis on genetic variables across species and regions indicated general trends in the partitioning of genetic variation. A conceptual map with a worldwide overview of those regions where high levels of gene flow were reported and of other regions that were considered as effective barriers, is presented. As an aim to increase the number of reliable comparisons of genetic variables across species or regions and to increase the relevance of mangrove genetics for local conservation issues, recommendations on the molecular markers and on the sampling design of individuals and populations are given within a conceptual context of evolutionary significant units.

Keywords: Mangrove; Biogeography; Dispersal; Genetic diversity; Genetic structure; Gene flow; Barrier; Conservation; Allozyme; RAPD; AFLP; ISSR; Chloroplast DNA; Microsatellite

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1. Introduction

The distribution of populations of mangrove tree populations is shaped by their response to colder climate and arid conditions at the limit of their ranges and therefore have been moving and expanding along changing coastal zones since the last glacial period, following a longer period of contraction of their ranges (Duke et al., 1998a,b; Saenger, 1998; Dodd et al., 2002). Detecting the patterns of such long-distance dispersal is a challenging research objective and allows to define evolutionary significant units and propagule dispersal routes, especially on basis of distinct chloroplast DNA variants. Such haplotypic chloroplast genomes were separated for a long period during the Pleistocene, but expanded along distinguishable routes on continents and islands. Understanding the historical factors that shaped the present-day populations is important for understanding the evolution of mangrove populations and predicting their likely response to climate change (Dodd et al., 2002). The extent and patterns of genetic diversity in natural mangrove populations are largely unknown across the species ranges except for a few *Avicennia* species (Maguire et al., 2002; Arnoud-Haond et al., 2006; Nettel and Dodd, 2007).

Several excellent and inspiring papers on the global biogeography and evolutionary aspects of mangrove trees appeared during the last decade. Patterns of genetic diversity, though at that time only available for a limited number of *Avicennia marina* (Forsk.)Vierh. populations (Duke, 1995) were discussed in the context of continental drift as a driver of tectonic gene dispersal of mangrove trees in geological times (>60 MYA). Measures of genetic identity, determined by enzyme electrophoresis were used by assuming that recent progenitor-derivatives have less variation than their progenitor. Saenger (1998) put forward the idea that the species composition of modern mangrove plants is largely a relict of historical processes, though these plants are subject to the climatic and geographical conditions of today. The modern mangrove flora on different continents shows a divergence between the Indo-Pacific and the Atlantic coastal zones. Paleontological studies shed more light on the possible time frame of mangrove evolution and distribution. Plaziat et al. (2001) estimated that the modern mangrove ecosystem and biogeographical split was established since the late Eocene (ca. 40 MYA). The discontinuity in the distribution of many mangrove species has become an attractive research subject and allowed interpretations on the origins of such unusual global patterns. Differentiation in epicuticular wax composition of *Rhizophora*, *Avicennia* and *Laguncularia* species from both West Africa and the South American Atlantic coast, gave evidence to suggest that mangroves from the latter region are a derivative of the former (Dodd et al., 1998). An inspiring essay on the disjunct nature of globally distributed mangrove trees raised many ideas on how to explain such an unexpected occurrence of restricted dispersal and gene flow, within widespread species of, e.g. *Rhizophora* (Duke et al., 2002).

At the range edges of a species (e.g. in *A. marina*) a decrease in allelic diversity was found, accompanied with a stronger genetic structure and inbreeding events when compared to populations in the core of the distribution range. This is suggested to be attributed to low effective population size, pollinator scarcity and higher environmental pressures at such range borders (Arnoud-Haond et al., 2006). Combined effects of founder events and enhanced local gene flow (e.g. in *Aegiceras corniculatum* (L.) Blanco; Ge and Sun, 1999) as opposed to low probability of long-distance dispersal (e.g. in *Avicennia germinans* (L.) Gaertn.; Nettel and Dodd, 2007) might be hypothesized as a more general pattern. Local deviations in gene diversities and differentiation of the averaged values in a species also might occur after disturbances of various origins, such as habitat fragmentation and isolation of estuaries in urban environments and associated pollution of sediments (Melville and Burchett, 2002), thereby altering locally the amount and distribution of genetic diversity. Local effects are custom, because highly significant actual gene flow (>30 migrants per generation) is usually within distances as short as a few tens of kilometres (Duke et al., 1998a,b) whereas effective barriers to gene flow (<1 migrant per generation) are at much larger distances. Historical gene flow, however, might have reached thousands of kilometers (Nettel and Dodd, 2007). Thus, the paradigm of mangrove tree distribution, namely the inferred ability of long-distance dispersal of well-adapted propagules in contrast to the accumulating data on sharp disjunct patterns of genetic diversity remains an attractive source of challenging hypotheses.

It is an intention of this review to summarize conceptually the recently published biogeographical considerations, opinions and thoughts, but it is highly recommended to read the original well-elaborated versions. The latest review on molecular data in mangrove trees dates back several years (Schwarzbach and Ricklefs, 2001) and placed emphasis on both protein and DNA data. The future outlook as they stated it in 2001, was that molecular methods would play an expanding role in mangrove plant research. About 50 papers on the subject appeared during the period 2000–2007 which is more than a doubling as compared to 1986–1999 (<20 papers), herewith following on average the steady increase of articles on molecular ecology in general during that period (3-fold increase), but a much stronger increase than on mangroves in general (1.5-fold increase).

In this review, most – if not all – recent studies on the molecular ecology of mangrove trees are discussed in the light of usefulness of particular techniques and approaches for a thorough analysis of this combined field with ecological and genetical relevance. The objective of this review is to present in an analytical way the recent history of such studies in mangrove trees and shrubs, not only at larger scales but also at regional and local scales. The most convenient way to structure this review, comprising various approaches in molecular ecology, including different species from many parts of the world and using different methods for calculating genetic variability, was to consider first the different types of molecular information with an emphasis on mangrove papers and issues, and secondly highlighting the various kinds of biogeographical information.

2. Methodological and technical considerations

Case-studies on isozymes, dominant markers, haplotypes and codominant microsatellite markers will be subsequently discussed in a context of feasibility, usefulness and perspectives for improvement, including personal opinions and practical considerations. Acronyms are explained, but for more information on the different techniques, their advantages, disadvantages and explanations of the genetic terminology or abbreviations used, I hereby refer to the many recent textbooks available in the field of population genetics (Hartl and Clark, 2007), molecular ecology (Beebee and Rowe, 2004) and ecological genetics (Lowe et al., 2004).

2.1. Isozymes and the stressful marine environment

Isozymes are electrophoretic variants of an enzyme, expressed in the tissue (mostly leaves are used) at the very moment of collection. Much care is needed during collection and transportation to the lab to maintain the activity of the enzymes until their separation after electrophoresis and subsequent substrate-specific staining of all variants. In practice, this means that one either collects branches with leaves and tries to keep these alive (e.g. in plastic bags exposed to light but not direct sunlight) or to collect single leaves and store these in plastic ziplock bags on ice. Upon arrival, enzymes should be extracted from the leaves and analysed immediately. Alternatively, these must be frozen in liquid nitrogen and further stored, either in liquid nitrogen or at −80 °C (never as high as −20 °C and never unfreeze and freeze again). This is crucial because most allozyme variants will denature at different rates and might lose their activity necessary for detection on a relatively thick gel medium of acrylamide or starch, requiring high amounts of the active enzyme. Cellulose acetate plates are less commonly used but have an advantage of requiring less volume of extract. The abovementioned precautions hindered the development of knowledge on isozyme polymorphism in mangrove trees during an era where many such studies were conducted on plants, including many seagrasses (e.g. McMillan, 1982) and aquatic plants (e.g. Triest, 1991a). The field conditions in the tropics do not always allow such careful handling. Though not reported in literature, there most likely were attempts in several labs throughout the world to reveal active enzymes from mangrove tissues. However, another obstacle for successful analysis of enzyme polymorphism in mangrove species are the secondary metabolites which denature the enzymes during grinding in an extraction buffer, as internal membranes of cell compartments disintegrate and allow contact between those compounds (e.g. phenols, tannins, etc.) and the enzymes. Such secondary metabolites are found in all tissues of most mangrove species and are thus difficult to avoid by searching for alternative tissues than mature leaves. Generally in tree leaves, problematic compounds can be neutralized by adding products that prevent enzymes from oxidation, e.g. polyvinylpyrrolidone (PVP), however, this requires systematic analysis of different concentrations and combinations of such additives, albeit an empirical search for suitable conditions to keep allozymes active. Goodall and Stoddart (1989) reported on such techniques to assess variation within fourteen enzyme systems in *Rhizophora* species, revealing 28 putative loci. A further analysis of five widely separated populations of *Rhizophora stylosa* Griff. showed only little geographic variation. A uniform genetic structure also was observed in isozymes of *Ceriops tagal* (Pers.) C.B. Robinson var. *tagal*, var. *australis* C.T. White and *Ceriops decandra* (Griff.) Ding Hou in northern Australia (Ballment et al., 1988). Isozyme patterns in *A. germinans* were also used to indicate similarities between regions, e.g. western Gulf of Mexico and Texas or dissimilarities, e.g. between the latter regions with Florida and eastern Caribbean (McMillan, 1986). A large-scale isozyme study across Australia, New Zealand, New Caledonia and from western Australia towards Thailand revealed that each of the considered *A. marina* varieties also corresponded to a particular gene flow grouping (Duke et al., 1998a,b). Again, as mentioned above, there most likely were more labs involved in trials on isozyme variability of sufficient enzyme loci, however, experiencing major difficulties to interpret the enzyme patterns in terms of true genes and alleles or resulting in no polymorphism at all.

Similar low or absent enzyme polymorphism was found in seagrasses such as *Zostera* (e.g. Gagnon et al., 1980; De Heij and Nienhuis, 1992; Williams and Orth, 1998), *Posidonia* (Capiomont et al., 1996) and in saltwater tolerant *Ruppia* species (Triest and Symoens, 1991). These aquatic plant groups are thought to display rather low genetic variability, due to extensive clonal spread (McMillan, 1991; Triest, 1991b) and limited hydrophilous pollination (Les, 1988). Both explanations are unlikely for many mangrove trees that are known to be highly sexual. Both the lack of resolving power and low genetic variability in genes coding for enzymes, actively expressed in leaf tissues, were at the basis of the general suffering to address questions on the genetic structuring of populations and the relationships with geographical and environmental factors. In general, aquatic plants have lower gene diversities than terrestrial plants when considering their enzymes (Hamrick and Godt, 1989; Triest, 1991a). Similar conclusions can be put forward, namely that mangrove trees are enzymatically very uniform when compared to their counterpart, the terrestrial tropical trees that exhibit the highest gene diversities in angiosperms (Hamrick and Godt, 1989). However, the number of case-studies in mangrove populations is not sufficient to allow a significant comparison. Such a more general hypothesis, as stated here – namely flowering plants from saline aquatic environments have lower enzyme polymorphism in their populations – should be further tested with DNA polymorphism, e.g. single nucleotide polymorphism (SNPs) in coding regions of enzyme genes. A comparative study of the genetic divergence of mangrove lineages from terrestrial relatives, already suggested that mangrove diversity is limited by evolutionary transition into the stressful marine environment (Ricklefs et al., 2006).

A particular stress factor for mangrove trees can be the rooting in contaminated sediments of estuaries close to urbanized areas. After assessing the allozyme variability within and among populations of *A. marina* in estuaries of Sydney, Australia, the resulting variability of different age-classes on clean and contaminated sediments was estimated by Melville and Burchett (2002) and Melville et al. (2004). Though it might remain difficult to interpret allozymes accurately in terms of genes and alleles, the presence–absence of each distinguishable allozyme allowed further multivariate approaches of both diversity and differentiation along the same coastline but under different habitat conditions. Allozyme distribution and patterns in leaf morphological attributes appeared to be very similar and allozyme differentiation corresponded to geographic distance (Melville and Burchett, 2002). Although only three groups at a distance of about 20, 60 and 80 km were available for comparison, it could be inferred that limitation in gene flow influenced the allozyme frequencies rather than the selection pressures imposed by the sediment characteristics. More diversity was observed in non-contaminated *A. marina* sites. Three age classes in clean and contaminated sediments showed greater allozymic differentiation among age classes than among sampling sites, however not related to the sediment metal or nutrient levels (Melville et al., 2004). They put forward that genetic distances within a mangrove habitat along a polluted river may reflect past fluctuations in pollution pressures, rather than age-classes as observed in subpopulations from a clean habitat.

Genetic variability analysis based on allozymes are extremely rare for mangrove trees and when achieved, relatively low levels of allelic polymorphism and heterozygosities were revealed, e.g. an expected heterozygosity *He* of 0.026 in *A. corniculatum* (Ge and Sun, 1999). Goodall and Stoddart (1989) found little polymorphism in Australian *R. stylosa* Griff. in only two out of the 28 enzyme loci and very low levels of heterozygosity ($He = 0.033$) were reported for *Kandelia candel* (L.) Druce in Hong Kong (Sun et al., 1998). A nearly complete lack of allozyme variation was found in four out of five investigated species of *Avicennia* (Duke et al., 1998a,b), with *A. marina* var. *marina* ($He = 0.0$–0.132) and related Australian varieties ($He = 0.025$–0.217) as an exception to this overall poverty of enzyme polymorphism in the genus. With expected heterozygosities $He = 0.0293$ and high gene flow levels of $Nm = 3.85$, *Bruguiera gymnorrhiza* (L.) Lamk. populations along the coast of China, present one of the few examples of outcrossing species that combine high rates of sexual reproduction with high amounts of propagule dispersal (Ge et al., 2005).

Allozymes remain reliable codominant markers of expressed genes (Table 1) and thus still have a future in mangrove genetics when field conditions allow careful handling of the collected tissues and when banding patterns of sufficient enzymes can be interpreted in terms of genes and alleles. This coding of unambiguous genotypes allows a whole spectrum of population genetic analysis, comparisons with other factors (morphology, geographical distance and environmental features) and multivariate techniques for the exploration of trends. At all times, one must avoid the interpretation of allozymes as merely phenotypes of banding patterns.

2.2. Dominant markers for identification purposes: is it a one or a zero?

Dominant markers can be defined as DNA fragments, amplified from any plant tissue, that allow to interpret their distribution only in terms of presence–absence coding. Heterozygosities are not readily detectable, though in particular cases, the intermediate intensity of an amplified fragment might indicate a heterozygous condition. This is somehow feasible for observation when dealing with related progeny of known parental origin or in cases of first generation hybrids (F1's). Dominant markers became very successful because these are relatively low cost and do not require knowledge of targeted sequences in the genome of an organism (Table 1). Thus, similar primers (a nearly unlimited series) can be tested on any species without the need for large investments of developing molecular markers. Additionally, DNA techniques are more popular than isozymes because they require only small amounts of leaf or other tissues to be dried on silica, which is a tremendous simplification of the logistics in the field, during transportation and for storage.

Dominant markers such as randomly amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) have their advantages in standard lab procedures, fast procedures on full genomic DNA extracts, but have a major disadvantage in showing no heterozygotes for estimating, e.g. levels of inbreeding (Table 1). An outcome to avoid misinterpretation from searching dominant markers is to combine these with either restriction polymorphisms (PCR-RFLP, polymerase chain reaction followed by restriction fragment length polymorphism, i.e. restriction enzymes that cut

Table 1
Characteristics of molecular marker methods as used in mangrove studies

Characteristic	Allozymes	RAPD	AFLP	ISSR[c]	Microsattelite (SSR)	cpDNA sequences
Level of polymorphism[a]	Low	Medium	Medium	Medium	High	Medium
Dominance[b]	Codominant	Dominant	Dominant	Dominant	Codominant	Haplotypic[c]
Sequence information needed[a]	No	No	No	No	Yes	Yes
Non-invasive sampling[b]	No	Yes	Yes	Yes	Yes	Yes
Start-up costs[a]	Medium[c]	Low	High[c]	Low	High	High
Development costs[a]	Low	Low	Medium	Low	High	Medium
Development time[b]	None	Limited	Limited	Limited	High[c]	Medium[c]
Reproducibility[a]	Medium/high	Low	Medium	Medium	High	High
Integration between labs[c]	Medium	Low	Medium	Medium	High	High
Allelic richness[c]	++	+	+	+	+++	++
Heterozygosity[c]	+++	+	+	+	+++	(++) pop level
Gene flow[a]	+++	(+)	(+)	(+)	+++	++
Inbreeding[c]	+++	−	−	−	+++	−
Individual genotyping[a]	(+)	(+)	+	(+)	+++	−
Population differentiation[a]	+++	++	++	++	++	++
Hybridization[a]	++	++	++	++	+	++
Polyploidy[a]	+++	−	−	−	+	(+)[c]
Phylogeography[a]	−	−	(+)[c]	−	(+)[c]	+++
Phylogeny	(+)	−	−	−	(+)[c]	+++

(+++), excellent; (++), good; (+), moderate; (+), has been used; (−), unlikely to be used or useless.

[a] Adapted from Lowe et al. (2004).

[b] Adapted from Frankham et al. (2002).

[c] Added or adjusted in this review.

the amplified products) or with other methods (e.g. PCR-RFLP of chloroplast DNA or mitochondrial DNA) to infer the maternal inheritance. The latter is necessary to detect the species that acted maternally (egg cell contribution to the formation of zygote) in hybrid formation or to detect the dispersal routes of different variants. RAPD and AFLP are often used for genotyping individuals but have more limitations in phylogeny and large-scale studies due to the possibility of increased product homology (i.e. amplified products of similar length but not similar in their sequence). Difficulties might occur when scoring according to the intensity of the amplified products and creating a data matrix of ones and zeros. The number of amplified fragments and the repeatability of AFLP is clearly higher than for RAPD (Table 1). Mostly no true genetic analysis is performed on RAPD and AFLP data as the scoring of presence–absence of amplified fragments do not allow to quantitatively measure the gene diversities. Estimations of expected heterozygosities are possible when assuming panmixis (Lynch and Milligan, 1994) or when *a priori* assigning a certain degree of inbreeding. Sharing amplified bands can be used to produce a cluster or an ordination plot to show interrelationships between individuals or populations.

AFLP reveals an extremely large amount of polymorphic loci with amplified fragments, thereby increasing the probability that each individual lacks different series of fragments out of the nearly 1000 putative loci. The presence–absence way of interpretation allows to estimate average heterozygosities (mostly supposing an Hardy–Weinberg equilibrium and thus neglecting the reality of possible deviations due to inbreeding, drift or low sample sizes) at (sub)population and species level. The application of RAPD and AFLP, the latter developed for breeding studies, has been widely used. RAPDs are useful at initial stages of an investigation. Both RAPD and AFLP are controversial for use in phylogenetic and phylogeographic studies because the one-zero data matrix cannot be ordered. In gene diversity studies, problems of product homology determination exist and without detailed genetic analysis, the designation of a fragment to a locus may be equivocal (Lowe et al., 2004). Another type of dominant markers, Inter-simple sequence repeats (ISSRs) is increasingly applied since 2000, as it has the potential to show higher polymorphism than RAPD at lower costs than AFLP. However, ISSR have similar limitations for data analysis as the former dominant marker methods (Table 1). Basically, the method involves amplification of regions between adjacent, inversely oriented microsatellites using a single simple sequence repeat (SSR-) containing primer. RAPD, AFLP and ISSR are considered to be reliable methods in F1 hybrid detection or in confirming the absence of first generation hybrids (Table 1). The relevance of using dominant markers (RAPD, AFLP and ISSR) for assessing genetic diversity within and among individuals, subpopulations or populations within a considered area – usually much smaller than the species range – especially lies in providing ordination plots of individual genotype distances, clusters of (sub)populations on basis of their averaged genetic distances, analysis of molecular variance (AMOVA) within and between populations relative to the total, statistics and analogues tested by random permutation.

2.2.1. Species characterisation and relationships: can order be obtained out of the unordened?

Fingerprinting with dominant markers (RAPD, AFLP and ISSR) are elegant techniques when the studied species are much related and when these species occur in the same biogeographical region. Otherwise, the risk of encountering product homology increases and may underestimate the measures of diversity due to amplified DNA fragments of similar length that are not homologous or contain substantial amounts of single nucleotide substitutions and insertion–deletions. To avoid this disadvantage, the amount of fragments is often increased, however this is not a real solution to the problem as it also increases the probability of touching upon more fragments showing product homology. Despite these disadvantages, it appears feasible to use dominant markers to confirm the existence of a taxon (at species level or lower) and to infer their degree of relationship to a certain level. However, the resulting phenograms as UPGMA clusters (unweighted pair-wise grouping method using averages) rarely can be considered as phylogenetically very accurate methods when compared to the potential of sequence data for phylogenetic analyses (Table 1).

AFLP proved to be useful in several case-studies to ascertain the status of a species. A large-scale study of *A. germinans* across the Pacific coast (from Baja California to Peru), the Atlantic coast (from Bahamas to Brazil) and western Africa, supported the justification of a single species across these biogeographical regions (Dodd et al., 2002), thereby rejecting the concept of a separate species *Avicennia africana* P. Beauv. along the eastern Atlantic coast or even any other lower taxon differentiation. AFLP characterisation of mangrove tree species and their relationship was performed for *Heritiera formes* Buch-Ham., *Heritiera littoralis* Dryand. and *Heritiera macrophylla* Wall. from India (Mukherjee et al., 2003). RAPD based relationships in legume species from mangroves in India were studied beyond species level (in fact rather distant genera) in *Dalbergia spinosa* Roxb., *Derris heterophylla* (Willd.) Backer, *Derris indica* (all three belonging to the subfamily *Papilinoidea*e), *Caesalpinia crista* L. and *Cynometra ramiflora* L. (both of the subfamily *Caesalpinioidea*e), which evidently clustered the subfamilies and subclustered the two *Derris* species, alongside with delivering the expected species-specific markers (Jena et al., 2004). Within family, relationships of eleven *Rhizophora* species using RAPD and AFLP also evidently showed a high degree of genetic divergence among the taxa and supported the morphologically based classification at tribe, genus and species level, except for *Bruguiera* and *Rhizophora* (Mukherjee et al., 2004). Additionally, attempts with RAPD and AFLP across families showed the expected relationships of 31 mangrove species as known from classical taxonomy, though at this level of higher taxonomic ranks, many unrelated mangrove species form clusters (Mukherjee et al., 2006). This is not surprising because the problem of product homology and the larger amount of non-shared amplified fragments might increase substantially. RAPD and PCR-RFLP (of nuclear DNA and chloroplast DNA) of the tribe *Rhizophoreae* in trees from India showed that the within-species variability was low (from RAPD data) and that species divergence was more elucidated with chloroplast gene regions than with ribosomal DNA repeat units of the nuclear DNA (Lakshmi et al., 2002). In my opinion, it is not recommended to use RAPD, AFLP or ISSR for constructing phylogenetic trees of taxa at species level and higher unless supplemented with sequences of chloroplast genes or other informative nuclear intron or exon sequences.

2.2.2. Straightforward hybrid detection though F1's remain hard to find

Hybrid mangrove trees and intermediate morphologies may present problems when there is a need to accurately identify for both field relevées as for *a posteriori* herbarium taxonomy. The existence of hybrids is mostly inferred from morphology by inventorying intermediate features or encountering putative hybrid vigour. Though hybridisation is supposed to occur between several mangrove tree species (Duke, 1984; Zhou et al., 2005), relatively few studies have concentrated on the identification of hybrids in populations. For this purpose, dominant markers can be applied effectively when the parents (or representatives of the parental species) are known, because the first generation hybrids must show a combined or additive pattern of amplified DNA products. This imperatively becomes less valid when introgressive hybridisation took place.

Hybrids between *Rhizophora apiculata* Blume and *Rhizophora mucronata* Lamk. were detected with both RAPD and PCR-RFLP of mitochondrial DNA at the eastern coast of Tamil Nadu, India (Parani et al., 1997). Hybrid detection is facilitated when the interpopulational diversity of each species (as spatially separated pure ones) and of the F1 population is low, thereby enhancing the probability to observe overall unique markers at species level for subsequent targeted hybrid genotyping. The use of dominant DNA markers at species level can be ideal to identify the hybrid status of populations and especially of the seedlings and young trees that lack sufficient diagnostic features in their morphology at that developmental stage. Lakshmi et al. (2002) found with PCR-RFLP of chloroplast genes that *R. mucronata* was the chloroplast donor for a natural hybrid (Pichavaram, India). Clear discrimination between two species and their hybrids was not only successful in the abovementioned *Rhizophora*, but also in *Sonneratia* × *gulngai* N.C. Duke (=*Sonneratia lanceolata* Blume × *Sonneratia alba* Smith) and *Sonneratia* × *hainanensis* W.C. Ko in Hainan, China. The latter putative hybrids showed little morphological variation and turned out to be all F1's, respectively with *S. alba* J. Smith and *Sonneratia caseolaris* (L.) Engl. as parents for *Sonneratia* × *gulngai* and *S. alba* and *S. ovata* for *Sonneratia* × *hainanensis*. Introgressive hybridisation was not observed and neither hybrid type deserved the species status because these were not self-sustaining populations (Zhou et al., 2005). Putative morphological hybrids at individual level also may turn out to be representatives of morphological variable species instead of true genetic hybrids. This was found in mixed populations of *Bruguiera sexangula* (Lour.) Poir. and *B. gymnorrhiza* along the western Sri Lankan coast (Abeysinghe et al., 2000). No hybrid *Bruguiera* individual was detected with RAPD, despite intermediate flower characteristics (Abeysinghe et al., 1999).

Similarly, enzymes that show uniform patterns within a taxon but high levels of genetic divergence among taxa, are very practical situations to detect whether or not hybridisation is involved in a morphological species complex e.g. *C. tagal* var. *tagal*, var. *australis* and *C. decandra*, that showed no sign of hybrid formation, even in sympatric areas (Ballment et al., 1988). On the other hand, closely related *Rhizophora* species are supposed to hybridize in sympatric areas, without showing distinct morphological forms, but as ecotypes with differing flowering period and niche specialisation, e.g. between *R. stylosa* and *R. mucronata* in the region from South East Asia to the North West Pacific Ocean and Northern Australia (Duke et al., 2002). In general, one could question whether pollination barriers mostly prevent formation of hybrids among related mangrove tree species. True hybrids are most likely rare and difficult to observe.

2.2.3. Gene diversities in small sample sizes from distant areas

Species that are widespread across oceans and continents, may include evidence on genetic diversity, genetic differentiation and genetic distance to illustrate the relative effects of continental drift; barriers for dispersal eventually resulting in cryptic species boundaries within the range of a morphological species; regional differentiation as a result of lowering of sea level during the recent Pleistocene glaciations; and ultimately provide evidence for conservation priorities at a regional scale. An extensive study carried out by Dodd et al. (2002) and Nettel and Dodd (2007) on the genetic diversity of *A. germinans* using AFLP amongst other markers, revealed that long-distance dispersal remains a valid hypothesis for this species. Although the number of rare and unique AFLP fragments was significantly higher for populations along western Africa when compared to those of the eastern Atlantic and western Pacific, these authors found a closer relationship of the former with French-Guinean populations. This suggests historical gene flow events over long distances, even when low. UPGMA clustering and unrooted NJT (neighbour joining tree) between pairs of populations gave sufficiently high bootstrap supports for accepting a major division between Atlantic and Pacific populations. The close relationship between *A. germinans* from western Africa and the eastern Atlantic coast was supported better when adding populations from Brazil. In my opinion, this indicates that the choice of sampled populations has an important influence on the interpretation of dominant markers especially when using small sample sizes, ranging from 4 to 20 per site, for conducting large-scale studies across oceans.

ISSRs have often been applied for the comparative study of genetic variability of mangrove populations across large geographical ranges. Despite the often low sample size of a population (10–20 individual mangrove trees), when pooled into regions, significant differences in genetic diversity estimates between regions were obtained. When the distribution area of a species is not fully covered (or with a non-representative subsampling) and only very distant populations across continents are compared, then the obvious and mostly *a priori* expected outcome with dominant markers is that clearly divided clusters per geographical region will be obtained from the calculated genetic distances, e.g. in *H. littoralis* Dryand. from China and Australia with sample sizes 10–20 per site (Jian et al., 2004); in *C. decandra* (Griff.) Ding Hou from East Malaya, West Malaya, southernmost Malaya and North Australia with sample size 7–22 per site (Tan et al., 2005); in *Lumnitzera racemosa* Willd. from the South China sea, East Indian ocean and North Australia with sample sizes 6–16 (Su et al., 2006) and similar areas (sample size 16–24) plus Sri Lanka (sample size 2) for *Lumnitzera littorea* (Jack) Voigt (Su et al., 2007); *C. decandra* (Griff.) Ding Hou (sample size 6–22), *C. tagal* (Perr.) C.B. Robinson (sample size 8–20) from the east and west coast of Thailand and the distant island Hainan (Ge and Sun, 2001), *C. tagal* (sample size 8–16) from the South China sea, East Indian ocean and North Australia, with sufficient bootstrap values in the NJT (Huang et al., 2007). Similarly for RAPD and ISSR, many studies were on low sample sizes, e.g. RAPD of *Acanthus ilicifolius* L. (sample size 5–7 in eight populations) and *Excoecaria agallocha* L. (sample size 12 in seven populations) along the east and west coast of peninsular India (Lakshmi et al., 1997; Lakshmi et al., 2000); *R. apiculata* Blume (10 samples in six populations) from India with one deviating population showing low polymorphism, most likely due to small sample sizes (Lakshmi et al., 2002); and ISSR in *S. alba* J. Smith from five populations in Hainan Island, China (Li and Chen, 2004).

The use of dominant markers is less appropriate for inferring reproductive strategies, outcrossing rates and local patterns of gene flow, due to the absence of heterozygote detection—a prerequisite for calculating deviations from the equilibrium. Nevertheless, a few attempts were made on mangrove trees to explore such possibilities. *A. corniculatum* from Hong Kong and other sites in southern China, showed substantial genetic differentiation in ISSRs between populations despite the relatively high levels of polymorphism (sample size of 15 individuals in 10 populations). This species has a mixed-mating to outcrossing system and the observed patterns might indicate the rare success of dispersal, however with sufficient gene flow through water-dispersed seedlings, thereby maintaining high diversities in the local populations (Ge and Sun, 1999). High levels of RAPD polymorphism were observed in *B. sexangula* (sample size 18–23 in three populations) from Southwestern Sri Lanka (Abeysinghe, 2000). Five populations of *A. germinans* along the coast of Mauretania (sample size 18–22) also showed high levels of polymorphism with only a moderate differentiation ($F_{ST} = 0.186$) at 60 km distance (Abeysinghe, 2000). At a very local scale, e.g. the disjunct zonation pattern of *A. marina* in Gazi bay (Kenya) RAPD allelic frequencies were used to observe significantly deviating frequencies between these two subpopulations. This fine-scaled approach allowed to demonstrate that seaward and landward populations (sample size 37) may have significantly different allele frequencies – four out of 48 – in each habitat, suggesting that restricted gene flow is possible at distances as short as 300 m (Dahdouh-Guebas et al., 2004). At a much shorter distance of only 100 m, *R. mucronata* showed no significant differences between a seaward sand ridge and a somewhat more landward site within Gazi bay (Abeysinghe, 2000).

Avicennia is the most studied genus among mangrove trees whereas the gene diversity assessment in other tree species was approached mainly once in a case-study. A thorough AFLP study combined with codominant SSR markers (see further) was achieved on *A. marina* in Australia (Maguire et al., 2002). AFLP was considered as a reliable and fast technique for delivering a large amount of marker fragments (nearly 1000) to distinguish individuals, thereby rendering AFLP useful in applied programs such as the monitoring of propagation in nurseries and identifying duplicates in collections. Besides providing a huge number of multilocus genotypes at individual tree level, AFLP also allowed to separate (sub)populations because of lower amounts of variance at higher geographical levels. AFLP thus revealed a large amount of putative loci of which a large proportion is polymorphic, i.e. the absence of an amplified fragment, indicating strong genetic structure with one group of populations in close vicinity being more related to each other than to other groups at larger geographical distances, sometimes including a ‘‘deviating’’ population due to lower sample size, e.g. *A. marina* in northern (sample sizes of 24–25), central (11) and (11–27) southern Vietnam (Giang et al., 2003); *A. germinans* along the Colombian coast with sample sizes of 10–12 in four populations though corrected for small sample sizes (Cerón-Souza et al., 2005); *Pelliciera rhizophorae* Triana & Planchon along the Colombian coast with samples sizes of 8–10 in six populations (Castillo-Cárdenas et al., 2005).

A meta-analysis of total gene diversities estimated from sufficient AFLP markers in *A. marina* (Maguire et al., 2000a,b; Giang et al., 2003), *A. germinans* (Dodd et al., 2002; Cerón-Souza et al., 2005; Nettel and Dodd, 2007) and *Pelliciera rhizophorea* (Castillo-Cárdenas et al., 2005) reveals that, on average, groups of central populations have *He* around 0.2 or higher, whereas a group of peripheral populations has *He* <0.1. Large-scale studies including both central and peripheral populations show intermediate values (Fig. 1). When adding more peripheral populations to a study, the total gene diversity of the species tend to become lower. There also seems to be a relationship (no significant positive correlation) between the considered percentage of polymorphic loci and their respective gene diversities (Fig. 2). A low proportion of polymorphic loci as well as a low gene diversity was found in a group of populations at the edge of a species range.

In my opinion, and based on the sampling strategies as argued by Lowe et al. (2004), dominant marker studies to infer long-distance dispersal in mangrove trees should be conducted with a sufficient large sample size (e.g. 20 or more individuals per population) because the mean number of alleles per gene is low to very low in mangroves trees. The sampling design should cover as much as possible the geographic range of the considered species because the aim is to detect unique alleles that are often at very low frequencies. Alternatively, a larger sample size per population (e.g. 30–50) for a coastal transect, covering only a part of the species range, is required for genetic structure analysis, local patterns of diversity, differentiation and inferring gene flow within metapopulations at a few hundreds of kilometers distance. Much criticism is necessary when trying to estimate gene diversities and genetic structuring of mangrove tree populations from few individuals in few populations at large distances (>1000 km), though such exploratory studies may evoke some new ideas to be tested.

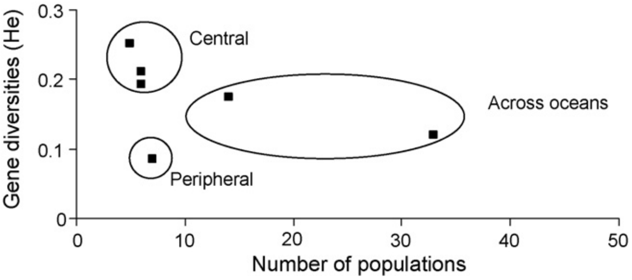

Fig. 1. Gene diversities for the total population in relation to the number of populations studied from central, peripheral and global ranges on basis of AFLP data from Dodd et al. (2002), Maguire et al. (2002), Giang et al. (2003), Cerón-Souza et al. (2005), Castillo-Cárdenas et al. (2005) and Nettel and Dodd (2007).

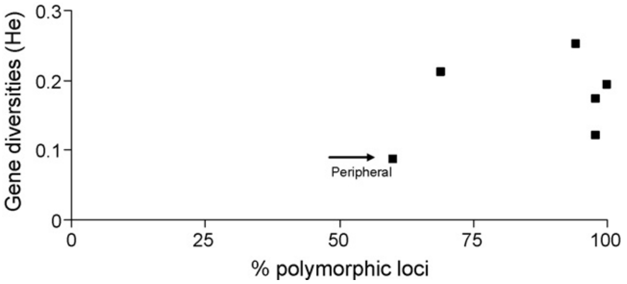

Fig. 2. Gene diversities for the total population in relation to their polymorphic loci on basis of AFLP data from Dodd et al. (2002), Maguire et al. (2002), Giang et al. (2003), Cerón-Souza et al. (2005), Castillo-Cárdenas et al. (2005) and Nettel and Dodd (2007).

2.3. Codominant microsatellite markers: highly variable but not in all species

Microsatellite markers, also named SSR (simple sequence repeats) are short tandem repeats of mono- to tetra-nucleotide repeats, which are assumed to be randomly distributed in the nuclear genome. Such SSRs are relatively abundant and have high mutation rates in comparison to other markers, which make them useful for various types of population studies (Lowe et al., 2004). An enormous advantage is that the exact designation of alleles (their length) to a known locus allows to standardise information between laboratories thereby making worldwide studies fully integrative (Table 1). This is not feasible with RADP, AFLP and ISSR. In mangrove trees, only recently the development of SSRs in a few species could facilitate studies on the molecular ecology of their populations with a much greater accuracy than allozymes and with much more analytical power than the dominant markers at both the individual level and for the *a priori* grouped assemblages of (sub)populations. The sample size needed to have a 95% probability of encountering at least one copy of each allele in a gene depends heavily on the frequency of the rarest allele in the population. At sample sizes of 50 individuals, this probability is reached in a two-allelic system if the most common allele has a frequency of 0.95 (Lowe et al., 2004). In most SSR loci, the most common allele has a lower frequency, thereby making it possible to detect more than two alleles at sample sizes as low as 50 individuals per population.

2.3.1. Allelic and genetic diversity in Avicennia microsatellites

Sixteen SSR primers were developed for *A. marina* by Maguire et al. (2000b). Three of these were used in a large-scale study with gene diversities *He* ranging from 0 to 0.85. Reduced values were towards the extremes of the species range, e.g. southern Africa, southern Australia and Japan (Maguire et al., 2000a,b). Such lower levels can be the result of founder effects and environmental constraints. Additional studies on *A. marina* from the northern edge of its range in Vietnam, showed a narrower range of *He* values (0.23–0.40 with population sizes from 11 to 30) in four SSR loci (Giang et al., 2003) and lowered *He* values (0.09–0.35), with population sizes from 19 to 34) when using seven SSR loci (Arnoud-Haond et al., 2006), thereby supporting the previous launched hypothesis on reduced gene diversity at range edges. Additional development of 10 microsatellite primers in *A. marina* and preliminary testing on 40 individuals in a population from Hainan, showed *He* values of 0.096–0.767 at locus level (Geng et al., 2007). The availability of 26 SSRs will allow even more accurate estimations of the allelic and genetic diversity in the near future. Despite this large amount of loci, the number of alleles per locus is often as low as two or three, thereby confirming the general opinion of low allelic diversity raised from earlier allozyme studies in mangrove trees. There is a high probability of encountering unique alleles combined with low or no polymorphism in some parts of the distribution range of *A. marina*. As the variable microsatellite regions were developed and initially selected for polymorphism in 15 individuals from three populations of Australian source material (Maguire et al., 2000b) and more recently from a Chinese source (Geng et al., 2007), this choice might potentially skew the resolution of revealing microsatellite polymorphism along other coastal areas such as South Africa (Dheopursad and Lamb, 2006). The absence of polymorphism in SSRs of Japanese populations might be indicative of this phenomenon resulting from biased initial screening. Out of the six polymorphic SSR loci, only one could be cross-amplified in four *Avicennia* species (*A. marina*, *Avicennia alba*, *A. rumphiana* Hallier f. and *A. officinalis* L.) but none in *A. germinans* (Maguire et al., 2000b), illustrating their limitation for a direct comparative analysis between several species, even when morphologically related. Six polymorphic microsatellite loci were *de novo* developed and made available for *A. alba* Blume which were tested on 36 individuals from the Mekong delta in Vietnam. Cross-amplification with *A. marina* revealed either monomorphic loci or no amplification at all (Teixeira et al., 2003). Ten polymorphic SSR loci were selected for *A. germinans*, of which nine also yielded amplification products in *Avicennia schaueriana* Stapf & Leech., five in *A. alba* and three in *A. marina* (Nettel et al., 2005) while six additional primers for *A. germinans* (Cerón-Souza et al., 2006) were developed from a source population in Puerto Rico. All these attempts clearly illustrate the extremely specific nature of microsatellites in the genomes of this genus and the need for additional microsatellite loci in search of sufficient polymorphism.

2.3.2. Microsatellite primer developments in several genera

Three out of the 10 SSR primers developed for *Rhizophora mangle* L. by Rosero-Galindo et al. (2002) were used by Arbeláez-Cortis et al. (2007) in five Colombian populations (populations sizes of 16–21). *He* values were high (0.601–0.725) but no unique alleles were detected. Genetic differentiation along the Colombian coast was low (R_{ST} values—analogous to F_{ST} were only 0–0.16), suggesting high amounts of gene flow, even over 400 km distance. SSRs for >10 species were recently published giving way to obtain more information on the diversity and genetic structuring of populations. Seven SSRs are available for *B. gymnorrhiza*, developed from Japanese source material, of which five SSR primers cross-amplified with *Bruguiera cylindrica* (L.) Blume and *Bruguiera parviflora* (Roxb.) Wright & Arnold ex Griff. (Sugaya et al., 2003); a single SSR with six alleles for *Kandelia obovata* Sheue, Liu & Yong from Japan (Harada et al., 2005); eight SSRs for *P. rhizophorae* Triana & Planchon from Colombia (Castillo-Cárdenas and Toro-Perea, 2007); five SSRs for *R. stylosa* (Islam et al., 2004), eight SSRs for *K. candel* (Islam et al., 2006a) and four SSRs, revealing 54 alleles in six populations of *K. obovata* and *K. candel* (Giang et al., 2006); and 10 additional primers for *B. gymnorrhiza* (Islam et al., 2006b); eight SSRs for *A. corniculatum* and nine SSRs for *S. caseolaris* from China (Chen et al., 2007a,b). Development of SSRs on these genera were achieved during the last years and still need to be validated in case-studies with ample materials to solve hypothesis driven research questions in the field of mangrove genetics.

2.4. Chloroplast DNA and mitochondrial DNA as clearcut haplotypic markers

Organel DNA mostly is maternally inherited but this should however not just be assumed but be tested for each species because exceptions to the ‘‘rule’’ might exist. Chloroplast DNA (cpDNA) is especially informative in phylogeny (e.g. maturase sequences of *matK* in Rhizophoraceae; Shi et al., 2002), species identification, phylogeography and hybrid detection (Table 1). Few population studies on mangrove trees involved chloroplast DNA, either sequencing variable intron regions or applying restriction enzymes (PCR-RFLP) to detect site variability. Lakshmi et al. (2002) found that *R. mucronata* was the chloroplast donor for a natural hybrid from Pichavaram, India. PCR-RFLP of cpDNA was applied for distinguishing species and estimating relationships in a few *Rhizophora*, *Ceriops* and *Bruguiera* species (Lakshmi et al., 2002). No differences in size and restriction patterns of cpDNA were found for *B. gymnorrhiza* and *B. sexangula* populations in distant sites of Southwestern Sri Lanka (Abeysinghe, 2000). PCR-RFLP of cpDNA was especially successful in a large-scale study of *A. germinans*, clearly separating phylogeographical regions such as Pacific coasts of Panama, Mexico, Costa Rica, Atlantic coasts along Central America, Florida, Caribbean coasts and the strikingly related haplotypes of the East Atlantic (French Guyana, Brazil) with those from western Africa (Nettel and Dodd, 2007).

Sequences of cpDNA were helpful in revealing phylogeographical patterns in *K. candel*, namely two distinct lineages – one in South China, Vietnam and East China Sea region

(Taiwan, Japan) and another in the southern China Sea region (Sarawak) – with low levels of genetic differentiation within each phylogeographical unit, indicating long-distance dispersal of maternal haplotypic variants across oceans between continents as well as island populations (Chiang et al., 2001). A study on a *matK* region of about 1500 bp length in *A. marina*, revealed that four indels (insertion–deletions) and two nucleotide substitutions distinguished Vietnam populations from those of Okinawa, Japan, whereas only one indel and one substitution separated populations from northern and southern Vietnam (Kado et al., 2004). *K. candel* also showed a clear haplotype discontinuity between northern and southern Vietnam (Kado et al., 2004), so there might be more mangrove species showing such distinct seed dispersal routes. Intraregional or intrapopulational cpDNA variation appeared to be low or absent. In some species there is no genetic variation in the *matK* region, e.g. *L. racemosa* from Vietnam and Japan (Kado et al., 2004). Rare and recently evolved cpDNA variants in *K. candel* were restricted to marginal populations in the northern part of Southwest Asia. CpDNA sequences in *C. tagal* revealed very different haplotypes (28 changes in nucleotides of two introns of totally 855 bp) on each side of the Malay Peninsula, a land mass considered as an actual and historical barrier to gene flow. The Indian Ocean haplotypes appear to be derived from the haplotypes present in the South China sea (Liao et al., 2007), though sample sizes were low (2–10 per population) and therefore is rather indicative than conclusive. Equally low sample sizes of <10 in a very similar study on *C. tagal* and *C. decandra*, using another intron of cpDNA revealed a similar pattern, namely the occurrence of different haplotypes from southern China, the South China Sea (Borneo, Malay Peninsula), the East Indian Ocean and northern Australia (Huang et al., 2007). Such a highly significant structure was attributed to the geological events during and just after the recent Pleistocene glaciation, when the maximum sea level dropped down to the Sunda Shelf. This land bridge separated the East Indian Ocean from the South China Sea refugia and allowed accumulation of different mutations in the cpDNA introns. It can be hypothesized that the closer relationship between *Ceriops* populations from Borneo and the Eastern Malay Peninsula could be the result of a gradual dispersal of propagules along the changing coastline of the gradually flooded Sunda Shelf at the end of the glaciation period. Additional phylogeographical information from cpDNA of mangroves across land or oceanic barriers most likely will be obtained in the near future.

3. Biogeographical patterns unravelled with molecular markers

The large range studies with AFLP and ISSR markers show that long dispersal distribution is possible (at least for *A. germinans*) and that genetic differences might correspond to a large biogeographical oceanic unit. Rather surprising is the observation that the ISSR and AFLP studies of populations from very distant locations – thousands of km – are not suffering from product homology and continue to provide evidence for the geographical separation at regional and oceanic level. This constancy can be attributed to the rather low regional genetic diversity within mangrove trees, thereby placing more emphasis on the interregional differences than the interpopulational levels. Up to now, none of such studies could demonstrate that pairwise genetic distances obtained from AFLP or ISSR were significantly correlated with the geographic distances.

A comparison of the gene diversity components *Ht* (total gene diversity), *Dst* (gene diversity between populations) and *Hs* (gene diversity within populations) of *C. decandra* (Huang et al., 2007), *L. racemosa* (Su et al., 2006), *L. littorea* (Su et al., 2007), *H. littoralis* (Jian et al., 2004), *C. tagal* (Huang et al., 2007) and *Ceriops australis* (Huang et al., 2007; Ge and Sun, 2001) revealed that most of the dominant marker based genetic diversity is between the populations for most cases (Fig. 3), except for *H. littoralis* and *C. australis*, most probably as a result of too low sample sizes or too restricted area of sampling in the latter. The importance of the sampled range is demonstrated with a meta-analysis of the molecular variance (AMOVA) and considered for three sets of literature data, i.e. the variance within a population, the variance between populations from the same coastline and the variance between distant populations across seas (Fig. 4). *Ceriops* species appear to have most of their variance across seas. Case studies with distant populations but from the same coastline show a large proportion of their molecular variance within the local populations, e.g. *C. australis* (Huang et al., 2007), *H. littoralis* (Jian et al., 2004), *P. rhizophorae* (Castillo-Cárdenas and Toro-Perea, 2007), *B. gymnorrhiza*, *B. sexangula* (Abeysinghe, 2000) and *A. germinans* (Abeysinghe, 2000; Dodd et al., 2002).

Though not conclusive with dominant markers for only a few species, these findings nevertheless indicate a more general pattern appearing in the distribution of genetic diversity of mangrove trees. It can be further hypothesized that when considering populations from the same coastline, the largest amount of genetic variation will be within the populations rather than between, which most likely is related to the dispersal routes of propagules along with prevailing water currents. When considering populations from different continents, opposite sides of a continent or a peninsula, and from islands then it can be hypothesized that the largest amount of genetic variation will be between the populations.

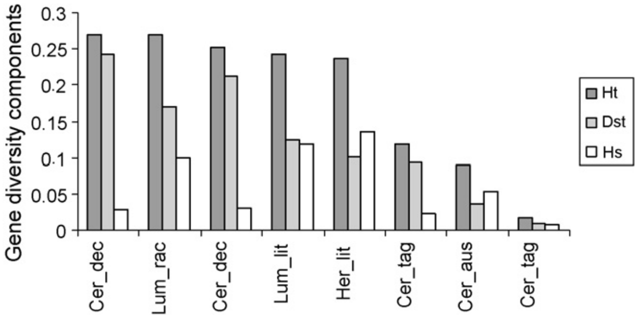

Fig. 3. Gene diversity components for total (*Ht*), between (*Dst*) and within (*Hs*) diversity of ISSR and AFLP markers from eight cases on six species—data from Ge and Sun (2001), Jian et al. (2004), Tan et al. (2005), Huang et al. (2007) and Su et al. (2007).

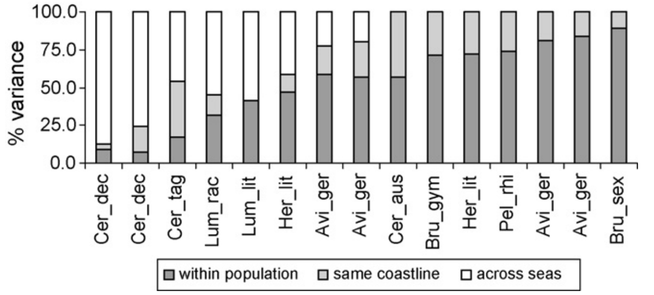

Fig. 4. Comparison of analysis of molecular variance results of ISSR and AFLP markers from 12 cases on nine species at three geographical levels—data from Dodd et al. (2002), Jian et al. (2004), Tan et al. (2005), Cerón-Souza et al. (2005), Castillo-Cárdenas et al. (2005), Su et al. (2006, 2007), Nettel and Dodd (2007) and Huang et al. (2007).

3.1. Do large oceanic barriers exist in AEP and IWP?

Two major disjunct patterns of mangrove distribution can be recognized. The Atlantic-East Pacific (AEP) with low species diversity (<10) and the Indo-West-Pacific (IWP) with higher species diversity in the Indo-Malaysian region (up to 40), though lower in the Western Indian Ocean (<10). The evidence of this difference between AEP and IWP is further supported by the absence of shared species, e.g. within the genera *Avicennia* (Duke, 1995) and *Rhizophora* (Duke et al., 2002). The richer biodiversity of the Indo-Malaysian region generally is explained by the more complex drift of tectonic fragments. The historical changes in the IWP are therefore considered to be more complex than in the AEP (Briggs, 1987). This hemispheric disjunction and the richer biodiversity in the IWP is generally accepted and no matter of debate. However, there are differing views on the importance of long-distance dispersal (LDD) to explain the actual distribution of species.

One view is that LDD remains limited because of major dispersal barriers, both land and water barriers (Duke et al., 2002), though this is species-dependent, with, e.g. *Rhizophora* being more mobile and having longer surviving propagules than *Avicennia*. Especially the idea that dispersal limitations can be finite across open water evoked an interest to study individual taxa across their entire distributional ranges for a better understanding of the earlier, historical dispersal of modern mangrove species. LDD ability is expected to vary with each taxon and there is a plea for coordinating genetic and morphological sampling (Duke et al., 2002). Establishment is primarily temperature limited whereas propagule dispersal is determined by ocean circulation patterns with cold water currents skewing the species range towards the equator and warm water currents towards or beyond the tropic of cancer or capricorn (Fig. 5). North equatorial ocean currents did not bring mangrove propagules to the Eastern Pacific Ocean islands despite available niche habitats. Land barriers such as the African continent and the Caribbean Atlantic Isthmus (CAI) are

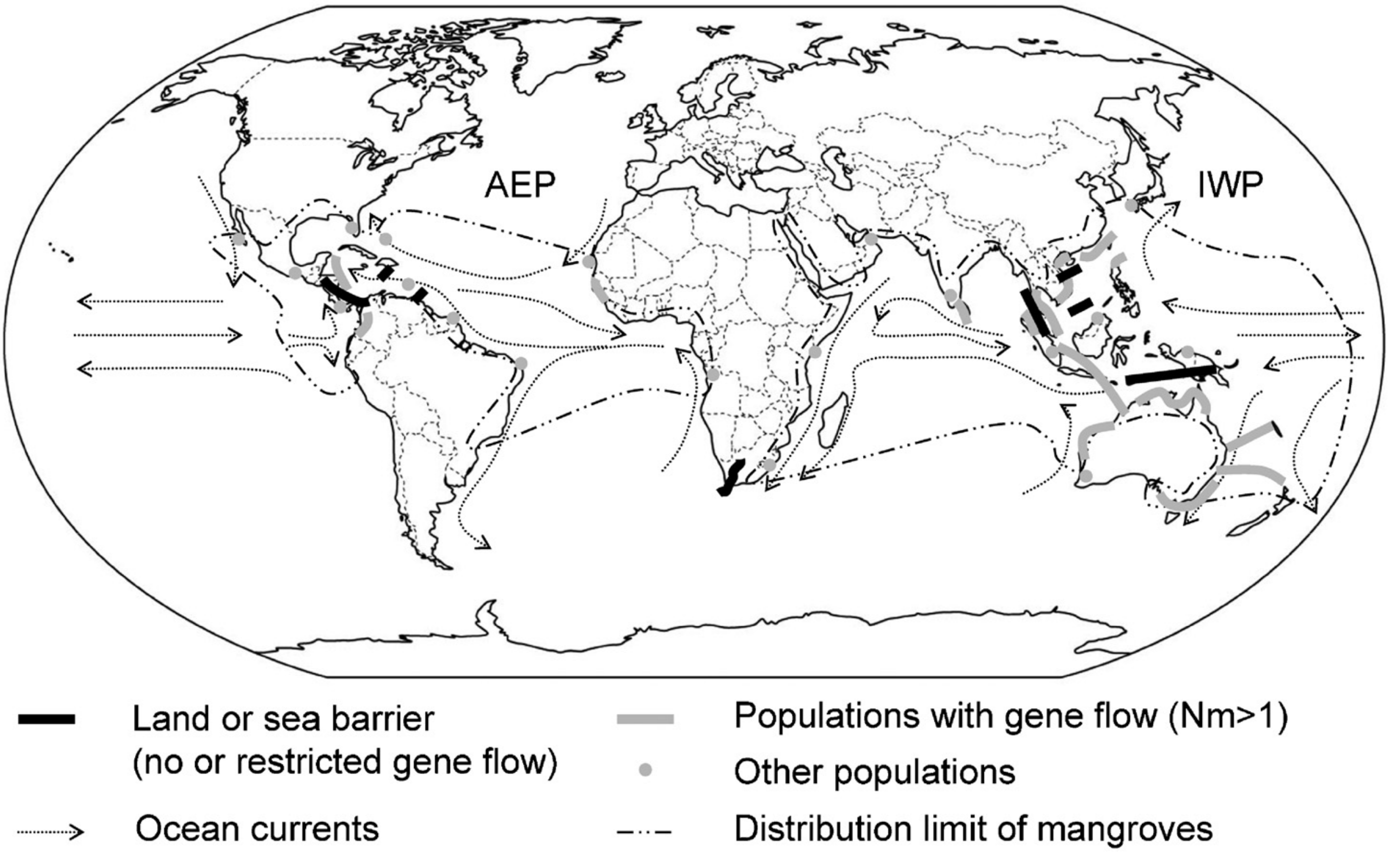

Fig. 5. Conceptual overview of land and oceanic barriers and of coastal zones with high levels of gene flow within the Atlantic East Pacific region and the Indo West Pacific (values and references are given in Tables 2 and 3).

generally accepted (Dodd et al., 2002; Duke et al., 2002; Nettel and Dodd, 2007). However, different views on basis of different taxa were raised on the importance of oceanic barriers in both AEP and IWP, i.e. the Atlantic Ocean separating West Africa from South America; the Western Indian Ocean and arid Middle East from the rest of the IWP; Australasia from the rest of the IWP (Fig. 5).

3.1.1. Trans-Atlantic dispersal

Duke et al. (2002) hypothesized both the Atlantic Ocean, though common species assemblages occur in the three subregions of the AEP (East Pacific, West Atlantic and East Atlantic) and the Indian Ocean to be an effective current barrier. Recent findings on *A. germinans* in the AEP were conclusive about the historical gene flow across the Atlantic. Dodd et al. (2002) and Nettel and Dodd (2007) found clear evidence for a close genetic relationship between populations from West Africa and South America using AFLP, cpDNA haplotypes and ITS sequences. Though Dodd et al. (2000) revealed closer similarities between populations of Atlantic South America and those of West Africa than with those of Atlantic North America, the resulting geographic pattern was still considered as ancient vicariance events (as put forward by Tomlinson, 1986; Duke, 1995). In the latter scenario, a higher degree of genetic differentiation should be observed after continental drift. When assuming historically more recent trans-Atlantic dispersal, only a low degree of genetic divergence should be expected. The large scale phylogeographical study of Nettel and Dodd (2007) confirmed such a scenario of historical LDD, most likely due to the strength and direction of the equatorial Atlantic ocean current during the Quaternary.

3.1.2. Barriers to dispersal and gene flow

Whereas the historical LDD across the Atlantic appears to be evident for *A. germinans*, such a LDD does not seem to hold for *A. marina* in the IWP (Maguire et al., 2000a,b; Duke et al., 2002). The Indian Ocean is considered as the only effective present-day barrier on basis of both species composition (East African mangrove communities are a subset of more species-rich mangroves in the East Indian Ocean and beyond) and of genetic evidence on *A. marina* across its range (Maguire et al., 2000a,b). A high number of unique alleles in each of the distant populations from South Africa, United Arabic Emirates, India and the Malaysian-Australasian region, allowed to put forward the idea of the Indian Ocean as a historical and present-day barrier. The historical changes of continental drift were more complex in the IWP than in the AEP (Briggs, 1987). Duke et al. (2002) suggested that current gene flow might exist between the Southeast Asian archipelago to Australasia and that exchange of genes through dispersal might occur in the EIO via India and Middle East. This then might correspond to a discrete metapopulation model to be expected along the coastal zone of the Middle East and Africa, following the southward Aguilhas ocean current. The existence of discontinuities in the distribution of taxa is used to support the idea that propagules are not so well adapted for long-distance dispersal (Duke et al., 1998a). However, this reasoning should not exclude the ability of LDD, but that sufficient gene flow (in fact seed flow) across the coastal areas is limited by the strength of particular equatorial counter currents and by the influence of large oceanic catchments.

On basis of the recent literature, one may conclude that several discontinuities exist in the IWP. Supported by evidence of absent gene flow (maternal seed flow) as detected especially with cpDNA, in addition to AFLP, ISSR and isozymes, the following barriers can be considered for further testing: between the EIO and Northern Australia; between New Guinea and Australia; between EIO and the Southern China Sea (SCS) due to the Malay peninsula land barrier; between SCS and Sarawak; between northern and southern Vietnam (Table 2, Fig. 5). Although the discontinuity in the Indian Ocean is supported by only one SSR study on *A. marina* (Maguire et al., 2000a,b), there is now ample evidence for restricted gene flow in the other Southeast Asian barriers for a number of species

Table 2
Evidence from literature on barriers and much restricted gene flow between regions (CAI = Central American Isthmus; CAR = Caribbean; EIO = East Indian Ocean; EP = East Pacific; ME = Middle East; NA = North Australia; SCS = South China Sea; WA = West Atlantic; WIO = West Indian Ocean)

Barrier	Gene flow	Species	Marker	Reference
CAI	Absent	*Avicennia germinans*	AFLP	Dodd et al. (2002)
CAI	Absent	*A. germinans*	cpDNA	Nettel and Dodd (2007)
WA vs. CAR	Restricted	*A. germinans*	cpDNA	Nettel and Dodd (2007)
EP (Mexico vs. Panama)	Absent	*A. germinans*	cpDNA	Nettel and Dodd (2007)
Malay Peninsula	Absent	*Ceriops tagal*	cpDNA	Liao et al. (2007)
Malay Peninsula	Absent	*Ceriops decandra*	ISSR	Ge and Sun (2001)
New Guinea vs. Australia	Restricted	*Avicennia marina*	Isozymes	Duke et al. (1998a,b)
EIO vs. NA vs. SCS	Absent	*C. tagal*	cpDNA	Huang et al. (2007)
EIO vs. NA vs. SCS	Absent	*C. decandra*	cpDNA	Huang et al. (2007)
EIO vs. SCS and Sarawak	Absent Restricted	*Kandelia candel*	cpDNA mtDNA	Chiang et al. (2001)
EIO vs. NA vs. SCS	Absent	*C. decandra*	ISSR	Tan et al. (2005)
EIO vs. NA vs. SCS	Restricted	*Lumnitzera racemosa*	ISSR	Su et al. (2006)
EIO vs. NA vs. SCS	Restricted	*Lumnitzera littorea*	ISSR	Su et al. (2007)
North vs. South Vietnam	Restricted	*A. marina*	cpDNA	Kado et al. (2004)
WIO vs. ME vs. EIO	Restricted	*A. marina*	SSR, unique A	Maguire et al. (2000a,b)

such as *A. marina*, *C. tagal*, *C. decandra*, *K. candel* and *L. racemosa* (references are in Table 2). Also in the AEP, besides the CAI as a land barrier, there is evidence of restricted gene flow on basis of cpDNA in *A. germinans* (Nettel and Dodd, 2007) along the coast of the East Pacific between Mexico and Panama; along the coast of the West Atlantic towards the Caribbean region; and along the Atlantic Central American coast (Table 2, Fig. 5).

3.1.3. Higher levels of gene flow along the same coastline

The present-day distribution of mangroves is the result of albeit recent shifts in ranges and range expansions after the last glacial maximum. These events undoubtedly account for the currently detected high levels of gene flow along the same stretch of a coastline. Much evidence on high levels of gene flow (i.e. values of $F_{ST} < 0.2$ or $Nm > 1$) became available with allozymes, ISSR and SSRs (occasionally with AFLP, RAPD or cpDNA sequences) on *A. germinans*, *A. marina*, *R. mangle*, *L. racemosa*, *B. gymnorrhiza*, *B. sexangula*, *H. littoralis*, *K. candel* and *A. corniculatum* (values and references are given in Table 3). High levels of gene flow could be observed along relatively short stretches along the same coast or across islands in the same region. In the AEP on average a moderate genetic structuring can be observed in distance classes <1000 km (Dodd et al., 2002), which suggests higher levels of gene flow at shorter distances, e.g. for *A. germinans* in the Caribbean sea between Mexico and Costa Rica; in the East Pacific along the Colombian coast; and along West Africa (Fig. 5, values and references in Table 3). In the IWP more species were studied than in the AEP and several showed at least a particular stretch with higher levels of gene flow: *B. sexangula* in southwestern Sri Lanka; *A. marina* in northern Vietnam or the northern Philippines; *B. gymnorrhiza*, *K. candel* and *A. corniculatum* along the South China coast; *L. racemosa* in northern Australia and *A. marina* in several neighboring regions of Australia or islands at the eastern distribution limits (Fig. 5, values and references in Table 3).

Up to now, there is no real evidence for an isolation by distance model, most probably due to either founder effects and range expansions following the last glaciation (Dodd et al., 2002) or due to higher levels of inbreeding in more isolated peripheral populations (Arnoud-Haond et al., 2006).

4. Molecular ecology in service of conservation and management

Despite their unique status as intertidal forests, hosting numerous faunal organisms (Nagelkerken et al., 2008; Cannicci et al., 2008) and providing essential functions and services to tropical and subtropical zones and their populations (Kristensen et al., 2008; Walters et al., 2008), mangroves are one of the world's most threatened ecosystems (Duke et al., 2007). Retrospective studies document how mangroves have been degraded over time (Dahdouh-Guebas and Koedam, 2008; Ellison, 2008). Not only direct or indirect anthropogenic degradation (Farnsworth and Ellison, 1997; Alongi, 2002) but

Table 3
Evidence from literature on high levels of gene flow (F_{ST} or Nm) between populations of the same biogeographical area

Coastline	F_{ST}	Nm	Marker	Species	Reference
West Africa	0.192 0.177 (ϕ_{ST})	–	AFLP	*A. germinans*	Dodd et al. (2002)
West Africa (Mauretania)	0.186	–	RAPD	*A. germinans*	Abeysinghe (2000)
Caribbean (Mexico-Costa Rica)	0.154 (ϕ_{ST})	–	AFLP	*A. germinans*	Dodd and Afzal-Rafii (2002)
New South Wales-New Caledonia	0.086	2.6	SSR	*A. marina*	Maguire et al. (2000a,b)
New South Wales–New Caledonia	–	>2–30	Allozymes	*A. marina*	Duke et al. (1998a,b)
Queensland-Northern Territory (Australia)	0.115	1.9	SSR	*A. marina*	Maguire et al. (2000a,b)
Queensland-Northern Territory (Australia)	–	>2–30	Allozymes	*A. marina*	Duke et al. (1998a,b)
Victoria-New South Wales (Australia)	0.154	1.4	SSR	*A. marina*	Maguire et al. (2000a,b)
Victoria-New South Wales (Australia)		1–2	Allozymes	*A. marina*	Duke et al. (1998a,b)
Victoria(Australia)-New Zealand	0.049	–	SSR	*A. marina*	Maguire et al. (2000a,b)
New South Wales (Australia)-New Zealand	0.100	2.2	SSR	*A. marina*	Maguire et al. (2000a,b)
New South Wales (Australia)-New Zealand		1–2	Allozymes	*A. marina*	Duke et al. (1998a,b)
Northern Territory (Australia)-Unit. Arab. Emir.	0.150	1.4	SSR	*A. marina*	Maguire et al. (2000a,b)
W. Australia-Thailand		1–2	Allozymes	*A. marina*	Duke et al. (1998a,b)
Northern Vietnam	0.06–0.20	–	SSR	*A. marina*	Arnoud-Haond et al. (2006)
Northern Philippines	Low	–	SSR	*A. marina*	Arnoud-Haond et al. (2006)
Northern Vietnam	Low	–	SSR	*A. marina*	Giang et al. (2003)
Southern Vietnam	Low	–	SSR	*A. marina*	Giang et al. (2003)
South China	–	High	cpDNA	*K. candel*	Chiang et al. (2001)
Australia (Daintree river)	–	1.92	ISSR	*Heritiera littoralis*	Jian et al. (2004)
South China (Hainan-Taiwan)	–	3.85	Allozymes	*Bruguiera gymnorrhiza*	Ge et al. (2005)
South China (Hong Kong-Hainan)	–	2.08	Allozymes	*Aegiceras corniculatum*	Ge and Sun (1999)
South China (Hong Kong-Hainan)	–	1.16	ISSR	*A. corniculatum*	Ge and Sun (1999)
Northern Australia	–	2.9	ISSR	*L. racemosa*	Su et al. (2006)
Southwestern Sri Lanka	0.105	–	RAPD	*Bruguiera sexangula*	Abeysinghe (2000)
East Pacific, Colombia	–	1.18–12.96	SSR	*Rhizophora mangle*	Arbeláez-Cortis et al. (2007)
East Pacific, Colombia	0.162	–	AFLP	*A. germinans*	Cerón-Souza et al. (2005)

also cryptic ecological degradation (Dahdouh-Guebas et al., 2005) and the increasing pressure of climatic change such as from sea-level rise (Gilman et al., 2008) jeopardises the survival of individual mangrove trees and of mangroves as a system. It becomes increasingly more important to understand the early drivers in mangrove establishment (Krauss et al., 2008), adult mangrove growth and development (Komiyama et al., 2008), and vegetation dynamics (Berger et al., 2008) in order to draft mangrove recovery programmes (Bosire et al., 2008).

A reasonable number of attempts were made in the field of molecular ecology of mangrove trees. Despite the tremendous efforts in collecting tree samples, analysing and treating the molecular data, only several outcomes became interpretable and hold promise for further hypothesis testing such as the phylogeographical patterns in *A. marina* and *A. germinans*. The genetic structuring of *A. marina* populations over its entire range is characterized by high overall F_{ST} values per SSR locus (0.25–0.52), supporting the idea that discrete populations are mostly differentiated but some of which show little differentiation, indicating some gene flow with $Nm > 1$ (Maguire et al., 2000a,b). In *A. marina*, most of the variation is partitioned among the populations of a large-scale distribution than among individuals within subpopulations (Maguire et al., 2000a,b). A similar partitioning of the variation could be observed at regional scale such as the coastal zone of Vietnam (Giang et al., 2003). *A. marina* populations located at the edge of their distribution area in North Vietnam were found to be strongly structured for SSR loci, combined with low gene diversities, indicating that high inbreeding levels occur (Arnoud-Haond et al., 2006). The gene flow is supposed to be low between such peripheral *A. marina* populations. Loss of genetic diversity may occur in heavily impacted areas and the transfer of germplasm can be envisaged for too fragmented and isolated populations (Su et al., 2007).

Allozymes, though still proven to be useful codominant markers in local studies on a few species (especially on the outcrossing *B. gymnorrhiza*), might be replaced by microsatellite markers in the near future, despite all encountered difficulties in the very specific and *de novo* development of suitable primer regions and screening for polymorphic loci. Sufficient SSRs are now available for *A. marina*, *A. germinans*, *S. caseolaris*, *A. corniculatum*, *B. gymnorrhiza*, *P. rhizophorae* and *K. candel* to perform detailed studies in the field of molecular ecology and testing hypothesis about reproductive strategies, age-class differences, pollination systems (pollen flow), mating systems (inbreeding, mixed, outcrossing), dispersal of propagules (seed flow) at various distance classes, considering putative historical dispersal routes and phylogeographical patterns that originated in changing coastal landscapes since the last glaciation period.

Schwarzbach and Ricklefs (2001) predicted a large impact of mangrove genetics, especially for conservation and management issues. Molecular data would provide insights in the genetic structure of populations for conserving and protecting genetic variation. Seven years later, my conclusion is that there still is a long way to go before reaching these practical goals on conservation and management of populations despite the outstanding studies on hemispheric and oceanic level that gave new insights on biogeographical and distributional patterns. Defining ecological significant units (ESU's), potentially to be considered also as management units for conservation, to detect hotspots of genetic diversity, primarily based on the haplotype

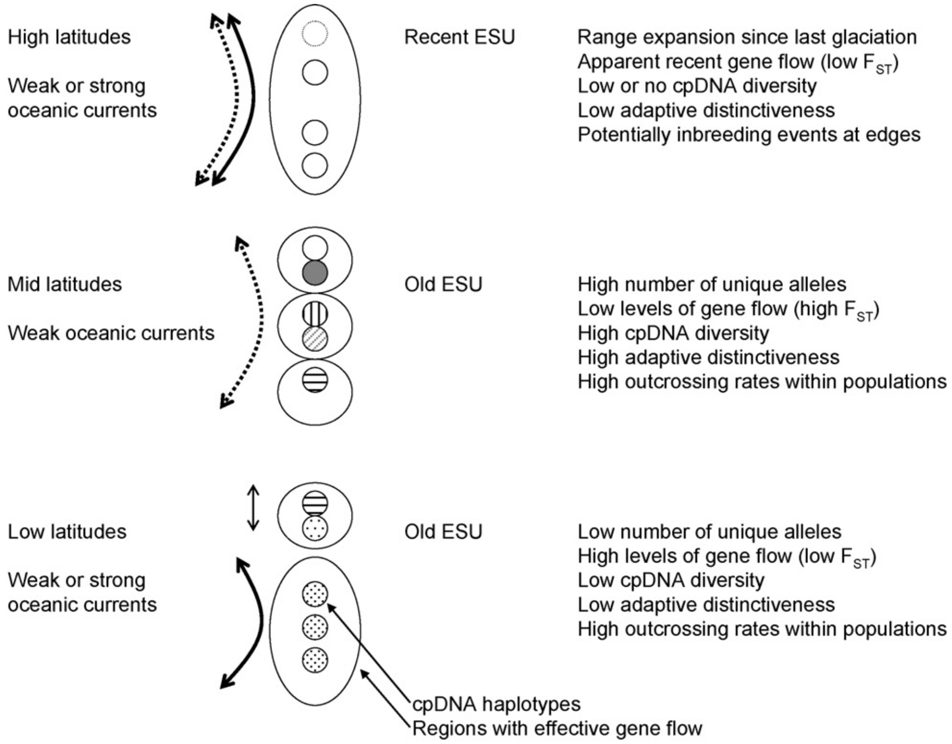

Fig. 6. Conceptual model for latitudinal distribution of evolutionary significant units (ESU) and putative features of genetic variables in mangroves along coastlines.

diversity reflecting historical seed dispersal across regions, remains an important task. The extent of each distinguishable ESU might depend on the latitudinal position of the populations within a species range and is supposed to be influenced by ocean currents, thereby potentially stretching or mixing the ESU's with unique alleles. An attempt to conceptually summarize the idea of ESU's could inspire future studies (Fig. 6). ESU's should be tested for distinctiveness in evolutionary timeframe, local (or regional) adaptation and local inbreeding events.

As can be inferred from this review, several studies considered low numbers, either a low number of individuals per population, low amounts of interpretable polymorphic loci and low amounts of populations or comparisons between few and distant mangrove populations. The low sample sizes in several studies certainly are related to the difficult conditions for collecting leaves of distant trees in hardly accessible inner parts of mangrove forests. For reasons of both scientific rigidity and potential opportunities in making generalisations, it is recommended in the field of mangrove genetics to give also priority to targeted research – thus less explorative – on few, well-known species, using 5–10 highly polymorphic SSR loci (>10 if only two to three alleles per locus); >10 populations when two groups are compared and up to 50 individuals per population when local dynamics such as pollen flow, paternity testing or inbreeding are envisaged. This design would allow testable hypotheses on, e.g. significant differences of gene flow between populations or inbreeding events within a restricted part of the species range but highly relevant for local conservation at province or country level.

Large-scale investigations should aim to collect the geographical and ecological range of the species, preferably a few from the centre and more from the periphery. Increasing the number of populations and sampling fewer individuals per population is an option (Lowe et al., 2004). Nevertheless, placing emphasis on either within or among populations must be determined by the life strategy of the species being studied and the problem investigated. Though very attractive and meaningful, large-scale analysis of a species should not be the scientific goal of every researcher as this requires concerted efforts to be successful. Well-designed local studies are equally challenging and are easier to achieve from a logistic point of view. Mangrove genetics will then become even more acceptable and applicable in discussions and negotiations on mangrove conservation and management with various stakeholders. Clearance of mangroves for other land uses, wood extraction and shrimp pond operation are causing threats to the maintenance of sufficient gene diversity in outcrossing or mixed mating species. This concern for conservation, both for maintenance of existing variation and considering indigenous source materials for replantation projects will be of major importance in future mangrove management plans. Reforestation programmes (Bosire et al., 2008) should take into account at least the possibilities of distinct cpDNA haplotypes and the existence of evolutionary significant units to be considered as management units (Liao et al., 2007), still visible through the maternally inherited features. Careful protection is needed against deliberate plantations across distant geographical locations using unknown source materials with an unknown genetic background. Such plans need consideration of breeding and naturalness for reasons of adaptiveness to local conditions of climate, flooding, sediment type, species interactions etc. Sufficient genetic variation should be maintained in smaller mangrove areas and in marginal populations of species at the edge of their natural range, as these appear to be subject to genetic erosion. Additionally, detection of gene diversity hot spots (many alleles, much heterozygosity) or unique genotypes (unique alleles), either within a region, country or worldwide, will be a necessary argument, among many others, to convince decision makers to preserve and protect such unique biogenetic reserves.

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References

Abeysinghe, P.D., 2000. Conservation genetics of mangroves: morphology and DNA polymorphism in a geographical context. PhD Thesis. Faculty of Science, Vrije Universiteit Brussel.

Abeysinghe, P., Triest, L., De Greef, B., Koedam, N., Hettiarachchi, S., 1999. Genetic differentiation between *Bruguiera gymnorhiza* and *B. sexangula* in Sri Lanka. Hydrobiologia 413, 11–16.

Abeysinghe, P.D., Triest, L., De Greef, B., Koedam, N., Hettiarachchi, S., 2000. Genetic and geographic variation of the mangrove tree *Bruguiera* in Sri Lanka. Aquat. Bot. 67, 131–141.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Arbeláez-Cortis, E., Castillo-Cárdenas, M.F., Toro-Perea, N., Cárdenas-Henao, H., 2007. Genetic structure of the red mangrove (*Rhizophora mangle* L.) on the Colombian Pacific detected by microsatellite molecular markers. Hydrobiologia 583, 321–330.

Arnoud-Haond, S., Teixeira, S., Massa, S.I., Billot, C., Saenger, P., Coupland, G., Duarte, C.M., Serrão, E.A., 2006. Genetic Structure at range edge: low diversity and high inbreeding in Southeast Asian mangrove (*Avicennia marina*) populations. Mol. Ecol. 15, 3515–3525.

Ballment, E.R., Smith, T.J., Stoddart, J.A., 1988. Sibling species in the mangrove genus *Ceriops* (Rhizophoraceae), detected using biochemical genetics. Aust. Syst. Bot. 1, 391–397.

Beebee, T., Rowe, G., 2004. An Introduction to Molecular Ecology. Oxford University Press, Oxford.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Briggs, J.C., 1987. Antitropical distribution and evolution in the Indo-West Pacific Ocean. Syst. Zool. 36, 237–247.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Capiomont, A., Sandmeier, M., Caye, G., Meinesz, A., 1996. Enzyme polymorphism in *Posidonia oceanica*, a seagrass endemic to the Mediterranean. Aquat. Bot. 54, 265–277.

Castillo-Cárdenas, M.F., Toro-Perea, N., 2007. Development and characterization of the first microsatellite markers in the mangrove species *Pelliciera rhizophorae* Triana & Planchon. Mol. Ecol. Notes 7, 1232–1234.

Castillo-Cárdenas, M.F., Toro-Perea, N., Cárdenas-Henao, H., 2005. Population genetic structure of neotropical mangrove species on the Colombian Pacific coast: *Pelliciera rhizophorae* (Pellicieraceae). Biotropica 37, 266–273.

Cerón-Souza, I., Toro-Perea, N., Cárdenas-Henao, H., 2005. Population genetic structure of neotropical mangrove species on the Colombian Pacific coast: *Avicennia germinans* (Avicenniaceae). Biotropica 37, 258–265.

Cerón-Souza, I., Rivera-Ocasio, E., Funk, S., McMillan, W., 2006. Development of six microsatellite loci for black mangrove (*Avicennia germinans*). Mol. Ecol. Notes 6, 692–694.

Chen, T., Zhou, R., Ge, X.J., Shi, S., 2007a. Development and characterization of microsatellite markers for a mangrove tree species *Sonneratia caseolaris* (L.) Engler (Lythraceae sensu lato). Conserv. Genet., doi:10.1007/s10592-007-9404-1.

Chen, G.Q., Li, L.F., Hao, G., Shi, S.H., Ge, X.J., 2007b. Characterization of seven genomic and one dbEST-derived microsatellite loci in the river mangrove *Aegiceras corniculatum* (Myrsinaceae). Conserv. Genet., doi:10.1007/s10592-007-9327-x.

Chiang, T.Y., Chiang, Y.C., Chen, Y.J., Chou, C.H., Havanond, S., Hong, T.N., Huang, S., 2001. Phylogeography of *Kandelia candel* in East Asiatic mangroves based on nucleotide variation of chloroplast and mitochondrial DNAs. Mol. Ecol. 10, 2697–2710.

Dahdouh-Guebas, F., Koedam, N., 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: A review. Aquat. Bot. 89, 80–92.

Dahdouh-Guebas, F., De Bondt, R., Abeysinghe, P.D., Kairo, J.G., Cannicci, S., Triest, L., Koedam, N., 2004. Comparative study of the disjunct zonation pattern of the grey mangrove *Avicennia marina* (Forsk.) Vierh. in Gazi Bay (Kenya). Bull. Mar. Sci. 74, 237–252.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

De Heij, H., Nienhuis, P.H., 1992. Intraspecific variation in isozyme patterns of phenotypically separated populations of *Zostera marina* L. in the southwestern Netherlands. J. Exp. Mar. Biol. Ecol. 161, 1–14.

Dheopursad, D., Lamb, J.M., 2006. Genetic Diversity of the mangrove *Avicennia marina*, in South Africa. S. Afr. J. Bot. 72, 340–1340.

Dodd, R.S., Afzal-Rafii, Z., Fromard, F., Blasco, F., 1998. Evolutionary diversity among Atlantic coast mangroves. Acta Oecol. 19, 323–330.

Dodd, R.S., Afzal-Rafii, Z., Bousquet-Mélou, A., 2000. Evolutionary divergence in the pan-Atlantic mangrove *Avicennia germinans*. New Phytol. 145, 115–125.

Dodd, R.S., Afzal-Rafii, Z., 2002. Evolutionary genetics of mangroves: continental drift to recent climate change. Trees 16, 80–86.

Dodd, R.S., Afzal-Rafii, Z., Kashani, N., Budrick, J., 2002. Land barriers and open oceans: effects on gene diversity and population structure in *Avicennia germinans* L. (Avicenniaceae). Mol. Ecol. 11, 1327–1338.

Duke, N.C., 1984. A mangrove hybrid, *Sonneratia* × *gulgnai* (Sonneratiaceae) from north-eastern Australia. Austrobaileya 2, 103–105.

Duke, N.C., 1995. Genetic diversity, distributional barriers and rafting continents—more thoughts on the evolution of mangroves. Hydrobiologia 295, 167–181.

Duke, N.C., Ball, M., Ellison, J., 1998a. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecol. Biogeogr. Lett. 7, 27–47.

Duke, N.C., Benzie, J.A.H., Goodall, J.A., Ballment, E.R., 1998b. Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-West Pacific. Evolution 52, 1612–1626.

Duke, N.C., Yuk Ying Lo, E., Sun, M., 2002. Global distribution and genetic discontinuities of mangroves—emerging patterns in the evolution of *Rhizophora*. Trees 16, 65–79.

Duke, N.C., Meynecke, J.-O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Ellison, J.C., 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: A review. Aquat. Bot. 89, 93–104.

Farnsworth, E.J., Ellison, A.M., 1997. The global conservation status of mangroves. Ambio 26, 328–334.

Frankham, R., Ballou, J., Briscoe, D., 2002. Introduction to Conservation Genetics. Cambridge University Press, Cambridge.

Gagnon, P.S., Vadas, R.L., Burdick, D.B., May, B., 1980. Genetic identity of annual and perennial forms of *Zostera marina* L. Aquat. Bot. 8, 157–162.

Ge, X.J., Sun, M., 1999. Reproductive biology and genetic diversity of a cryptoviviparous mangrove *Aegiceras corniculatum* (Myrsinaceae) using allozyme and intersimple sequence repeat (ISSR) analysis. Mol. Ecol. 8, 2061–2069.

Ge, X.J., Sun, M., 2001. Population genetic structure of *Ceriops tagal* (Rhizophoraceae) in Thailand and China. Wetlands Ecol. Manage. 9, 203–209.

Ge, J.P., Cai, B., Ping, W., Song, G., Ling, H., Lin, P., 2005. Mating system and population genetic structure of *Bruguiera gymnorrhiza* (Rhizophoraceae), a viviparous mangrove species in China. J. Exp. Mar. Biol. Ecol. 326, 48–55.

Geng, Q.F., Lian, C.L., Tao, J.M., Li, S.Q., Hogetsu, T., 2007. Isolation and characterization of 10 new compound microsatellite markers for a mangrove tree species, *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae). Mol. Ecol. Notes 7, 1208–1210.

Giang, L.H., Hong, P.N., Tuan, M.S., Harada, K., 2003. Genetic variation of *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae) in Vietnam revealed by microsatellite and AFLP markers. Genes Genet. Syst. 78, 399–407.

Giang, L.H., Geada, G.L., Hong, P.N., Tuan, M.S., Lien, N.T.H., Ikeda, S., Harada, K., 2006. Genetic variation of two mangrove species in *Kandelia* (Rhizophoraceae) in Vietnam and surrounding area revealed by microsatellite markers. Int. J. Plant Sci. 167, 291–298.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Goodall, J.A., Stoddart, J.A., 1989. Techniques for the electrophoresis of mangrove tissue. Aquat. Bot. 35, 197–207.

Hamrick, J., Godt, M., 1989. Allozyme diversity in plant species. In: Brown, A., Clegg, M., Kahler, A., Weir, B. (Eds.), Plant population genetics, breeding and genetic resources. Sinauer, Sunderland, pp. 43–63.

Harada, K., Okaura, R., Giang, L.H., Huan, N.V., Iwasaki, M., Nitasaka, E., 2005. A novel microsatellite locus isolated from an AFLP fragment in the mangrove species *Kandelia obovata* (Rhizophoraceae). J. Plant. Res. 118, 49–51.

Hartl, D.L., Clark, A.G., 2007. Principles of Population Genetics, 4 ed. Sinauer, Sunderland, MA.

Huang, Y., Tan, F., Su, G., Deng, S., He, H., Shi, S., 2007. Population genetic structure of three tree species in the mangrove genus *Ceriops* (Rhizophoraceae) from the Indo West Pacific. Genetica, doi:10.1007/s10709-007-9182-1.

Islam, M.S., Lian, C., Kameyama, N., Wu, B., Hogetsu, T., 2004. Development of microsatellite markers in *R. stylosa* using a dual-suppression-polymerase chain reaction technique. Mol. Ecol. Notes 4, 110–112.

Islam, M.S., Lian, C.L., Kameyama, N., Wu, B., Hogetsu, T., 2006a. Development and characterization of ten new microsatellite markers in a mangrove tree species *Bruguiera gymnorrhiza* (L.) Lamk. Mol. Ecol. Notes 6, 30–32.

Islam, M.S., Tao, J.M., Geng, Q.F., Lian, C.L., Hogetsy, T., 2006b. Isolation and characterization of eight compound microsatellite markers in a mangrove tree *Kandelia candel* (L.) Druce. Mol. Ecol. Notes 6, 1111–1113.

Jena, S., Sahoo, P., Mohanty, S., Das, A.B., 2004. Identification of RAPD markers, *in situ* DNA content and structural chromosomal diversity in some legumes of the mangrove flora of Orissa. Genetica 122, 217–226.

Jian, S., Tang, T., Zhong, Y., Shi, S., 2004. Variation in inter-simple sequence repeat (ISSR) in mangrove and non-mangrove populations of *Heritiera littoralis* (Sterculiaceae) from China and Australia. Aquat. Bot. 79, 75–86.

Kado, T., Fujimoto, A., Giang, L.H., Tuan, M., Hong, P.N., Harada, K., Tachida, H., 2004. Genetic structures of natural populations of three mangrove species, *Avicennia marina*, *Kandelia candel* and *Lumnitzera racemosa*, in Vietnam revealed by maturase sequences of plastid DNA. Plant Species Biol. 19, 91–99.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Lakshmi, M., Rajalakshmi, S., Parani, M., Anuratha, C.S., Parida, A., 1997. Molecular phylogeny of mangroves I. Use of molecular markers in assessing the intraspecific genetic variability in the mangrove species *Acanthus ilicifolius* Linn. (Acanthaceae). Theor. Appl. Genet. 94, 1121–1127.

Lakshmi, M., Parani, M., Ram, N., Parida, A., 2000. Molecular phylogeny of mangroves VI. Intraspecific genetic variation in mangrove species *Excoecaria agallocha* L. (Euphorbiaceae). Genome 43, 110–115.

Lakshmi, M., Parani, M., Parida, A., 2002. Molecular phylogeny of mangroves IX. Molecular marker assisted intra-specific relationships in the Indian mangrove tribe Rhizophoreae. Aquat. Bot. 74, 201–217.

Les, D.H., 1988. Breeding systems, population structure, and evolution in hydrophilous angiosperms. Ann. Mo. Bot. Gard. 75, 819–835.

Li, H.S., Chen, G.Z., 2004. Genetic diversity of *Sonneratia alba* in China detected by inter-simple sequence repeats (ISSR) analysis. Acta Bot. Sin. 46, 515–521.

Liao, P.-C., Havanond, S., Huang, S., 2007. Phylogeography of *Ceriops tagal* (Rhizophoraceae) in Southeast Asia: the land barrier of the Malay Peninsula had caused population differentiation between the Indian Ocean and South China Sea. Conserv. Genet. 8, 89–98.

Lowe, A., Harris, S., Ashton, P., 2004. Ecological Genetics Design, Analysis and Applications. Blackwell, Oxford.

Lynch, M., Milligan, B.G., 1994. Analysis of population genetic structure with RAPD markers. Mol. Ecol. 3, 91–99.

Maguire, T.L., Saenger, P., Baverstock, P., Henry, R., 2000a. Microsatellite analysis of genetic structure in the mangrove species *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae). Mol. Ecol. 9, 1853–1862.

Maguire, T.L., Edwards, K.J., Saenger, P., Henry, R., 2000b. Characterization and analysis of microsatellite loci in a mangrove species *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae). Theor. Appl. Genet. 101, 279–285.

Maguire, T.L., Peakall, R., Saenger, P., 2002. Comparative analysis of genetic diversity in the mangrove species *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae) detected by AFLPs and SSRs. Theor. Appl. Genet. 104, 338–398.

McMillan, C., 1982. Isozymes in seagrasses. Aquat. Bot 14, 231–243.

McMillan, C., 1986. Isozyme patterns among populations of black mangrove, *Avicennia germinans*, from the Gulf of Mexico-Caribbean. Contrib. Mar. Sci. (Univ. Texas) 29, 17–25.

McMillan, C., 1991. Isozyme patterning in marine spermatophytes. Meise In: Triest, L. (Ed.), Isozymes in Water plants. Op. Bot. Belg., vol. 4. . National Botanic Garden of Belgium, pp. 193–200.

Melville, F., Burchett, M., 2002. Genetic variation in *Avicennia marina* in three estuaries of Sydney (Australia) and implications for rehabilitation and management. Mar. Pollut. Bull. 44, 469–479.

Melville, F., Burchett, M., Pulkownik, A., 2004. Genetic variation among age-classes of the mangrove *Avicennia marina* in clean and contaminated sediments. Mar. Pollut. Bull. 49, 695–703.

Mukherjee, A.K., Acharya, L.K., Mattagajasingh, I., Panda, P.C., Mohapatra, T., Das, P., 2003. Molecular characterization of three *Heritiera* species using AFLP markers. Biol. Plant. 47, 445–448.

Mukherjee, A.k., Acharya, L., Panda, P.C., Mohapatra, T., Das, P., 2004. Genomic relations among two non-mangrove and nine mangrove species of Indian Rhizophoraceae. Z. Naturforsch. 59, 572–578.

Mukherjee, A.K., Acharya, L., Panda, P.C., Mohapatra, T., 2006. Assessment of genetic diversity in 31 species of mangroves and their associates trough RAPD and AFLP markers. Z. Naturforsch. 61, 413–420.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Nettel, A., Dodd, R.S., 2007. Drifting propagules and receding swamps: genetic footprints of mangrove recolonization and dispersal along tropical coasts. Evolution 61, 958–971.

Nettel, A., Rafii, F., Dodd, R.S., 2005. Characterization of microsatellite markers for the mangrove tree *Avicennia germinans* L. (Avicenniaceae). Mol. Ecol. Notes 5, 103–105.

Parani, M., Rao, C.S., Mathan, N., Anuratha, C.S., Narayanan, K.K., Parida, A., 1997. Molecular phylogeny of mangroves III. Parentage analysis of a Rhizophora hybrid using random amplified polymorphic DNA and restriction fragment length polymorphism markers. Aquat. Bot. 58, 165–172.

Plaziat, J.-C., Cavagnetto, C., Koeniguer, J.-C., Baltzer, F., 2001. History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. Wetlands Ecol. Manage. 9, 161–179.

Ricklefs, R., Schwarzbach, A., Renner, S., 2006. Rate of lineage origin explains the diversity anomaly in the world's mangrove vegetation. Am. Nat. 168, 805–810.

Rosero-Galindo, C., Gaitan-Solis, E., Cardenas-Henao, H., Tohme, J., Toro-Perea, N., 2002. Polymorphic microsatellites in a mangrove species, *Rhizophora mangle* L. (Rhizophoraceae). Mol. Ecol. Notes 2, 281–283.

Saenger, P., 1998. Mangrove vegetation: an evolutionary perspective. Mar. Freshw. Res. 49, 277–286.

Schwarzbach, A., Ricklefs, R., 2001. The use of molecular data in mangrove plant research. Wetlands Ecol. Manage. 9, 195–201.

Shi, S., Zhong, Y., Huang, Y., Du, Y., Qiu, X., Chang, H., 2002. Phylogenetic relationships of the Rhizophoraceae in China based on sequences of the chloroplast gene *matK* and the internal transcribed spacer regions of nuclear ribosomal DNA and combined data set. Biochem. Syst. Ecol. 30, 309–319.

Su, G., Huang, Y., Tan, F., Ni, X., Tang, T., Shi, S., 2006. Genetic variation in *Lumnitzera racemosa*, a mangrove species from the Indo-West Pacific. Aquat. Bot. 84, 341–346.

Su, G., Huang, Y., Tan, F., Ni, X., Tang, T., Shi, S., 2007. Conservation genetics of *Lumnitzera littorea* (Combretaceae), an endangered mangrove from the Indo-West Pacific. Mar. Biol. 150, 321–328.

Sugaya, T., Yoshimaru, H., Takeuchi, T., Katsuta, M., Fujimoto, K., Changtragoon, S., 2003. Development and polymorphism of simple sequence repeat DNA markers for *Bruguiera gymnorrhiza* (L.) Lamk. Mol. Ecol. Notes 3, 88–90.

Sun, M., Wong, K.C., Lee, J.S.Y., 1998. Reproductive biology and population genetics of a viviparous mangrove species, *Kandelia candel* (Rhizophoraceae). Am. J. Bot. 85, 1631–1637.

Tan, F., Huang, Y., Ge, X., Su, G., Ni, X., Shi, S., 2005. Population genetic structure and conservation implications of *C. decandra* in Malay Peninsula and North Australia. Aquat. Bot. 81, 175–188.

Teixeira, S., Arnaud-Haond, S., Duarte, M., Serrão, E., 2003. Polymorphic microsatellite DNA markers in the mangrove tree *Avicennia alba*. Mol. Ecol. Notes 3, 544–546.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Triest, L. (Ed.), 1991. Isozymes in Water plants. Op. Bot. Belg., vol. 4. National Botanic Garden of Belgium, Meise.

Triest, L., 1991b. Enzyme polymorphism and its relationships to biological features in aquatic plants (including a comparison with terrestrial plants). In: Triest, L. (Ed.), Isozymes in Water plants. Op. Bot. Belg., vol. 4. National Botanic Garden of Belgium, pp. 201–240.

Triest, L., Symoens, J.J., 1991. Isozyme variation in populations of the submerged halophyte *Ruppia* (Ruppiaceae). In: Triest, L. (Ed.), Isozymes in Water plants. Op. Bot. Belg., vol. 4. National Botanic Garden of Belgium, pp. 115–132.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Williams, S.L., Orth, R.J., 1998. Genetic diversity and structure of natural and transplanted eelgrass populations in the Chesapeake and Chincoteague Bays. Estuaries 21, 118–128.

Zhou, R., Shi, S., Wu, C.-I., 2005. Molecular criteria for determining new hybrid species – An application to the *Sonneratia* hybrids. Mol. Phylogenet. Evol. 35, 595–601.

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Review

The habitat function of mangroves for terrestrial and marine fauna: A review

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Abstract

Mangroves are defined by the presence of trees that mainly occur in the intertidal zone, between land and sea, in the (sub) tropics. The intertidal zone is characterised by highly variable environmental factors, such as temperature, sedimentation and tidal currents. The aerial roots of mangroves partly stabilise this environment and provide a substratum on which many species of plants and animals live. Above the water, the mangrove trees and canopy provide important habitat for a wide range of species. These include birds, insects, mammals and reptiles. Below the water, the mangrove roots are overgrown by epibionts such as tunicates, sponges, algae, and bivalves. The soft substratum in the mangroves forms habitat for various infaunal and epifaunal species, while the space between roots provides shelter and food for motile fauna such as prawns, crabs and fishes. Mangrove litter is transformed into detritus, which partly supports the mangrove food web. Plankton, epiphytic algae and microphytobenthos also form an important basis for the mangrove food web. Due to the high abundance of food and shelter, and low predation pressure, mangroves form an ideal habitat for a variety of animal species, during part or all of their life cycles. As such, mangroves may function as nursery habitats for (commercially important) crab, prawn and fish species, and support offshore fish populations and fisheries. Evidence for linkages between mangroves and offshore habitats by animal migrations is still scarce, but highly needed for management and conservation purposes. Here, we firstly reviewed the habitat function of mangroves by common taxa of terrestrial and marine animals. Secondly, we reviewed the literature with regard to the degree of interlinkage between mangroves and adjacent habitats, a research area which has received increasing attention in the last decade. Finally, we reviewed current insights into the degree to which mangrove litter fuels the mangrove food web, since this has been the subject of long-standing debate.

Keywords: Mangrove; Habitat use; Fauna; Ecosystem interaction; Ecology; Biodiversity; Food web

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1. Introduction

Mangroves are predominantly intertidal habitats that occur worldwide in the (sub) tropics along sheltered and shallow-water coastlines. The prop-roots and pneumatophores of mangrove trees extend into the intertidal and subtidal where they become a rare feature: hard substrata in an otherwise soft sediment environment (Ellison and Farnsworth, 1992). As such, mangrove roots become home to terrestrial as well as marine plants, algae, invertebrates and vertebrates. Mangroves form a habitat for a wide variety of species, some occurring in high densities. They are productive habitats and may support coastal fisheries for prawns and fishes (Manson et al., 2005). Mangroves are also important to humans for a variety of reasons, including aquaculture, agriculture, forestry, protection against shoreline erosion, as a source of fire-wood and building material, and other local subsistence use (Hogarth, 1999; Walters et al., 2008). Worldwide, loss of mangroves has been significant in recent decades, although in some regions of the world mangroves still occur as very extensive forests (Spalding, 1998; Alongi, 2002). They suffer from direct impacts such as cutting and pollution, as well as from hidden impacts such as changes in inland freshwater management (Dahdouh-Guebas et al., 2005), and are often regarded as unpleasant environments with little intrinsic value.

Animals found within mangrove environments include a variety of taxa, many of which are vulnerable or threatened as a result of human activities in the coastal zone. Determining the value of mangroves and other estuarine habitats for these animals requires knowledge of their life history, physiology and ecology as they interact across the dynamic mosaic of available habitats. Evidence suggests that mangroves are important to these species, but a lack of research is a major impediment to an evaluation of their mangrove dependency. A challenge for future research is separating the roles of mangroves from those of estuaries and other shallow-water habitats, to help determine the appropriate temporal and spatial scales for habitat protection (see Manson et al., 2005). Estuarine habitats have been recognised as important drivers of nearshore fish productivity. Worldwide, about 30% of all commercial fish species are mangrove-dependent (Naylor et al., 2000), producing an annual catch of almost 30 million tonnes in 2002 (FAO, 2004). Of all ecosystems, estuaries have the highest value per hectare (Costanza et al., 1997), making it significant for subsistence in many coastal communities. In Bragança (N-Brazil), for example, 68% of the cash income is primarily derived from mangrove crabs and fish (Glaser, 2003).

Recent and extensive reviews on mangroves as habitats for terrestrial and marine fauna include Hogarth (1999), Kathiresan and Bingham (2001), and Qasim and Kathiresan (2005). Studies related to the linkages between mangroves and coastal fish populations and fisheries, and new insights relating to the debate on the degree to which mangrove litter fuels the mangrove food web, form an important body of work published since these reviews; hence there is the need for a more up-to-date review. The current review summarises the available data on mangroves as a habitat for terrestrial and marine fauna, with special reference to the interlinkages with adjacent habitats and the importance of litter in the mangrove food web. We focus on the main groups of animals found in the mangrove habitat: sponges, various groups of meiofauna and macrofauna (epifauna and infauna), prawns, insects, fishes (bony fishes and elasmobranchs), amphibians, reptiles, and birds, accepting that a review of the complete fauna would be too far-reaching for this special issue, and that some mangrove fauna are not discussed here. These include less-well studied taxa like zooplankton (e.g., Mohan and Sreenivas, 1998; Ferrari et al., 2003; Krumme and Liang, 2004), tunicates (e.g., Carballo, 2000; Goodbody, 2003; Rocha et al., 2005), and mammals such as bats (Bordignon, 2006), buffalo (Dahdouh-Guebas et al., 2006), deer (Barrett and Stiling, 2006), dolphins (Smith et al., 2006), flying foxes (Moore, 2002), manatees (Spiegelberger and Ganslosser, 2005), marsupials (Fernandes et al., 2006), otters (Angelici et al., 2005), primates (Nijman, 2000), rabbits (Forys and Humphrey, 1996), raccoons (Cuaron et al., 2004), and tigers (Gopal and Chauhan, 2006).

2. Mangroves as habitats for sponges

2.1. Diversity and distribution of sponges

Sponges occurring on mangrove roots are conspicuous because they often have large sizes (±50 cm in diameter or more) and brilliant colours (e.g., Rützler and Feller, 1996; Diaz et al., 2004). Although some encrusting mangrove sponges can survive above the water line for many hours during a tidal cycle (Barnes, 1999), the aquiferous system of larger sponges will collapse when emerged for periods longer than 4 h (Rützler, 1995). Considering the typical zonation of mangrove habitats (Nybakken, 1997), the mangrove area available to sponge communities is very small, especially when compared to the much larger adjacent subtidal habitats afforded by seagrass beds, hard-bottom areas, and coral reefs. In addition, while only prop-roots that extend below lowest low water (LLW) will support most sponge growth (Ellison and Farnsworth, 1992; Rützler, 1995), the vast majority of these roots are in water that is either too shallow or too stagnant. Most mangrove sponge assemblages are restricted to prop-roots that hang over tidal channels that cut through soft sediment habitats (e.g., Engel and Pawlik, 2005) or raised rock, rubble or peat banks that drop off abruptly to depths greater than LLW (e.g., Farnsworth and Ellison, 1996). These two types of shoreline are also accessible by boat and snorkelling, while the vastness of the remaining intertidal mangrove is not. Therefore, to infer that sponge-covered prop-roots are a common feature of mangrove habitats as a whole would be false. Nevertheless, where they occur, mangrove sponges form distinctive, high-biomass communities with associated fish and invertebrate faunas (Kathiresan and Bingham, 2001). For example, at Punta del Este, Cuba, Alcolado (1991) estimated 50–80 individual sponges per meter of shoreline, while at study sites in the Florida Keys, U.S.A., Engel and Pawlik (2005) counted 1195 sponges comprising ten species that occupied 73.5% of available mangrove root space.

The great majority of published information on mangrove sponge communities comes from the Caribbean rather than the Indo-Pacific (Barnes and Bell, 2002). There are probably several reasons for this disparity, related both to differences in the mangrove habitats and the sponge assemblages of the two regions. In the lower intertidal zone, Caribbean mangroves are dominated by *Rhizophora mangle*, which has long prop-roots that extend into deeper water and support a great diversity of epibiotic algae and invertebrates below the LLW line (Farnsworth and Ellison, 1996), while in most Indo-Pacific mangroves the equivalent zone is dominated by *Avicennia* and *Sonneratia* spp. which lack prop-roots (Nybakken, 1997). Unlike the large sponges found in Caribbean mangroves, Barnes (1999) found 91.9% of mangrove sponges from Mozambique were encrusting and the remainder were buried. The taxonomy of Caribbean sponges is much better described than sponges of the Indo-Pacific, and this has limited ecological studies of the latter. Caribbean sponge communities are remarkably similar over the breadth of the biogeographic region (see below), while those in the Indo-Pacific are more diverse and variable from location to location (van Soest, 1994).

There tends to be lower species diversity of sponges in mangroves than adjacent subtidal habitats (seagrass beds, coral reefs, hard-bottom, etc.) in both the Caribbean and Indo-Pacific (Barnes, 1999; Barnes and Bell, 2002). Numbers of sponge species can be high, ranging from 3 to 147 for Caribbean mangroves (Diaz et al., 2004), although these communities are usually made up of less than ten dominant species on the basis of biomass, and generally the same dominant species are found throughout the biogeographic area. Among the most common Caribbean species are *Tedania ignis*, *Lissodendoryx isodictyalis*, *Chondrilla nucula*, *Geodia gibberosa*, *Halichondria melanodocia*, *Haliclona manglaris*, *Dysidea etheria*, *Hyrtios proteus*, *Mycale microsigmatosa* and *Spongia tubulifera* (cf. Sutherland, 1980; Alcolado, 1991; Engel and Pawlik, 2005; Diaz et al., 2004). Too few studies exist to generate a similar list for Indo-Pacific mangrove sponges, but it is interesting that some of the same genera were represented in a survey of the Quirimba Archipelago of Mozambique (Barnes, 1999), where *Tedania digitata*, *Haliclona* sp. and *Biemna* sp. were found in mangrove habitats.

2.2. *Influence of abiotic factors on sponge communities*

As primarily nearshore, estuarine habitats, mangroves are strongly influenced by abiotic factors such as freshwater runoff, sedimentation, and rapid temperature fluctuations from the influence of sun and wind on tidally driven shallow water. After many years of studying communities around Kingston Harbour, Jamaica, Goodbody (1961) concluded that mangrove root communities seldom reach a climax condition because of mortality after intense rain events. Studies of mangrove sponge communities in the Florida Keys, U.S.A., have also documented yearly cycles of mortality associated with physical disturbance, temperature extremes and rain events (Bingham and Young, 1995; Pawlik et al., 2007). Quite the opposite was found for mangrove sponge communities at Bahía de Buche, Venezuela, which, despite having the same community structure as other Caribbean sites, was remarkably stable over time (Sutherland, 1980). This unusual situation can be attributed to a combination of little or no rainfall runoff or storm events at this site as well as constant annual temperatures (Sutherland, 1980).

The cline in abiotic effects as a function of proximity to the shore has best been demonstrated by Ellison and Farnsworth (1992), who documented the prop-root faunal assemblages at six sites in Belize, ranging from nearshore to offshore sites. Species richness of all epibionts increased with distance offshore, with only two sponge species present in the most nearshore site increasing to nine in the most offshore site. In a subsequent study of four mangrove islands in Belize, Farnsworth and Ellison (1996) found that sponge diversity and abundance was greatest on the leeward rather than the windward side of islands, which they attributed to a combination of abiotic (physical disturbance) and biotic (larval supply) factors acting at different spatial and temporal scales. Compared with sponges growing in other tropical subtidal habitats (i.e., seagrass beds and coral reefs), species that comprise the typical Caribbean mangrove sponge community are specifically adapted to survive extremes in salinity, temperature and sedimentation, either through tolerance or rapid recovery after catastrophic loss (Engel and Pawlik, 2005; Pawlik et al., 2007). Adaptations to abiotic extremes do not preclude mangrove sponges from living in habitats where physical conditions are better, such as reef habitats, but biotic factors, particularly predation, limit their distribution in those habitats (Pawlik, 1997; and see below).

2.3. *Influence of biotic factors on sponge communities*

While abiotic factors control the large-scale distribution of sponge assemblages in mangrove habitats, biotic factors may have important effects at smaller scales. Seastars of the genus *Echinaster* may be locally abundant in some Caribbean mangrove habitats, where they consume sponges on prop-roots that become accessible to them when they grow into the subtidal sediment (Waddell and Pawlik, 2000). Parrotfishes and angelfishes make excursions from reef habitats to some mangrove sites to feed on sponges (Dunlap and Pawlik, 1998). When the most common mangrove sponge species were transplanted to reef sites, they were quickly consumed by angelfishes, yet many of these same mangrove species can be found in interstices in the reef framework where predatory fishes cannot eat them (Dunlap and Pawlik, 1996; Pawlik, 1998). Therefore, mangrove habitats serve as a refuge from fish predation for sponges that are able to survive the abiotic conditions found there.

Competition for available stilt-root space within Caribbean mangrove sponge communities appears to be intense, with a clear dominance-hierarchy based on growth rate and the production of putative allelochemical agents (Engel and Pawlik, 2005). Interestingly, some mangrove sponges appear to use chemical cues to foster the growth of other sponge species on their surfaces, with the overgrowing species providing an anti-predatory chemical defence to the undefended species under them (Engel and Pawlik, 2000, 2005; Wilcox et al., 2002). While allelochemicals may be important in sponge–sponge interactions, Bingham and Young (1991) could find no allelochemical effect of existing mangrove sponges on other epifaunal invertebrate species in settlement experiments. Wulff (2005) recently suggested that the competitive superiority of mangrove sponges prevented the colonisation of mangrove sponge habitats by sponge species usually found in reef habitats. This conclusion, that biotic factors may be more important than abiotic factors in affecting mangrove sponge ecology, was based on transplantation experiments conducted in offshore mangrove habitats in Belize (Wulff, 2005), where Ellison and Farnsworth (1992) had previously found abiotic conditions were least stressful, and species richness was highest. In subsequent experiments at three coastal mangrove sites in the Florida Keys, U.S.A., and one offshore site on Grand Bahama island, Bahamas, Pawlik et al. (2007) observed that reef sponges declined in health and died within 60 days of being transplanted to mangrove sites, a result that was attributed to abiotic conditions of high temperature, rainfall events and sedimentation in mangrove habitats. While some mangrove sponge communities have been documented to be less influenced by abiotic factors, particularly freshwater runoff (Sutherland, 1980; Wulff, 2005), these are the exception rather than the rule (Goodbody, 1961; Ellison and Farnsworth, 1992; Bingham and Young, 1995; Farnsworth and

Ellison, 1996; Kathiresan and Bingham, 2001; Pawlik et al., 2007).

In addition to mutualisms between sponge species in mangrove habitats (Wilcox et al., 2002), sponges also form mutualisms with the mangrove plants themselves. Ellison and Farnsworth (1990, 1992) reported that epifaunal sponges and ascidians reduce damage to prop-roots of *R. mangle* by wood-boring isopods: roots without epifaunal cover exhibited damage and 55% lower growth relative to roots with epibiont cover. In addition, Ellison et al. (1996) discovered that transplantation of sponges onto prop-roots induced, within 4 weeks, the formation of fine rootlets that pervade sponge tissue.

Aside from the hard substratum provided by prop-roots, mangroves may also offer an enhanced food source for sponges. In general, sponges feed primarily on particles the size of bacteria. The rich microbial community that results from the productivity and nutrient cycling in mangroves (Kathiresan and Bingham, 2001) may promote faster sponge growth than in adjacent oligotrophic habitats, such as coral reefs.

3. Mangroves as habitats for meiofauna

3.1. Diversity and distribution of meiofauna

In mangroves a distinct 'phytal' meiofauna (generally defined as animals passing through a 1.0 or 0.5 mm sieve but retained on a 63 μm mesh), often dominated by acari, inhabits hard substrata such as prop-roots and pneumatophores (Proches et al., 2001; Bartsch, 2003). The focus of the majority of studies of meiofauna in mangroves, however, is on communities living in sediment or on decomposing leaves. Within mangrove sediments, as in most estuarine habitats, meiofauna are the numerically dominant metazoans. For practical purposes meiofauna may be split into hard-bodied and soft-bodied components (Somerfield et al., 2005). The former are organisms that preserve well in formalin and so can be identified in preserved samples. They are easier to study than the soft-bodied forms for which specialised preservation and examination techniques are required. Nematodes and harpacticoid copepods usually constitute over 90% of the hard-bodied component of the meiofauna and are the subject of most studies. Soft-bodied forms, such as Turbellaria, are generally ignored although they may be equally abundant (Alongi, 1987b).

Although a number of studies of meiofauna in mangrove habitats document the abundances of organisms identified to high taxonomic levels, such as phyla or classes, there are relatively few studies which provide information on the species composition and structure of meiofaunal communities. Species-level information for copepods is available from a geographically widespread set of mangrove systems with very different environmental characteristics, including a lagoonal system in Brazil (Gerlach, 1958; Por, 1984; Por et al., 1984), fringe mangrove forests in Florida (Hopper et al., 1973; Fell et al., 1975), hard-bottom mangroves in Sinai (Por, 1977; Reice et al., 1984), and soft-sediment tropical mangroves in India (Kondalarao, 1984; Kondalarao and Raman-Murty, 1988) and southern Malaysia (Sasekumar, 1994; Gee and Somerfield, 1997; Somerfield et al., 1998). The heterogeneity of systems studied makes it difficult to draw general conclusions about benthic copepods in mangroves. For example, reports of the number of species found in mangroves vary widely. Por et al. (1984) recorded 14 species from the mangrove system of Cananeia in Brazil. Kondalarao (1984) and Kondalarao and Raman-Murty (1988) found 32 and 22 species of harpacticoid copepods, respectively, from 2 estuarine mangrove systems in India. Sasekumar (1994) found 25 species in mangrove systems in Selangor, Southwest Malaysia. Between 60 and 70 putative species of Copepoda were recorded from the Merbok estuary in Northwest Malaysia (Somerfield et al., 1998). One reason for the relatively high number of species recorded in the latter study was that, as well as documenting sediment-dwelling species, it examined leaf-litter assemblages in detail. Particularly, a high number of species of the family Darcythompsoniidae, especially species of *Leptocaris*, were recorded. This family of copepods were only found on leaf litter, and appear to be adapted to feeding directly on litter, or for grazing epiflora off flat surfaces (Somerfield et al., 1998). Although there is little general evidence for a specialised mangrove copepod fauna, Por (1984) speculated that amongst the Darcythompsoniidae some specialised species might have evolved. The findings of Somerfield et al. (1998) support that speculation.

Species-level information on nematodes also comes from a heterogeneous set of mangrove environments which fall into two main groups: (1) seasonally arid, subtropical or temperate mangroves in Australia (Decraemer and Coomans, 1978; Hodda and Nicholas, 1986; Nicholas et al., 1991; Gwyther, 2003) and Brazil (Netto and Gallucci, 2003), and (2) tropical mangroves in Australia (Alongi, 1987a,b, 1990), India (Krishnamurthy et al., 1984), Malaysia (Gee and Somerfield, 1997; Somerfield et al., 1998) and eastern Africa (Ólafsson, 1995; Ólafsson et al., 2000). Neither Ólafsson (1995) nor Somerfield et al. (1998) found any evidence for a specialised nematode assemblage in mangrove sediments, as most of the genera found by them are typical of intertidal sediments worldwide. Estimates of the number of species inhabiting mangrove sediments vary widely. The number of nematode taxa found in the Merbok mangrove forest in Malaysia (107 putative species: Somerfield et al., 1998) compares well with numbers of nematode taxa from mangroves in Zanzibar (94 genera: Ólafsson, 1995) and Brazil (94 putative species, 86 genera: Netto and Gallucci, 2003), but is more than three times as many as were recorded from *Rhizophora* mangrove forests in Selangor, Malaysia (29 species: Sasekumar, 1994) or southern Australia (21 putative species: Gwyther, 2003). There are no nematode taxa which have been found exclusively on mangrove litter, but species in the genera most abundant on litter, such as *Diplolaimelloides*, *Diplolaimella*, *Atrochromadora* and *Theristus*, have been recorded in association with mangrove detritus from as far afield as Australia (Alongi, 1990; Nicholas et al., 1991), Southeast Asia (Gee and Somerfield, 1997; Somerfield et al., 1998; Zhou, 2001), Africa (Ólafsson, 1995) and Florida (Hopper et al., 1973).

3.2. *Influence of abiotic and biotic factors on meiofauna distribution*

Studies of meiofaunal distributions within mangrove sediments tend to highlight the importance of generalised intertidal and estuarine environmental gradients known to influence meiofaunal distributions everywhere, such as tidal height, salinity, oxygen availability, and sediment properties such as organic content and granulometry (Somerfield et al., 1998; Coull, 1999). Meiofaunal distributions are patchy, and vary seasonally (Alongi and Christoffersen, 1992), leading to widely varying estimates of abundance. The majority of individuals are concentrated near to the sediment surface, especially in muds (Somerfield et al., 1998), although in relatively oxic sandier sediments more specimens are found below the sediment surface (Vanhove et al., 1992). Siphonolaimid nematodes from genera such as *Parastomonema*, which contain chemosynthetic symbionts and are typically found in anoxic environments rich in methane, are known to occur in mangrove sediments (Somerfield et al., 1998; Kito and Aryuthaka, 2006). Ansari et al. (1993), working on an Indian mangrove mudflat, showed that meiofauna depth distributions correlated with vertical gradients in redox potential, but also with interstitial water content, organic matter content, adenosine triphosphate concentrations, phytobenthic abundance and bacterial counts.

The fact that different mangrove plants have different environmental niches, and affect their surroundings differently, makes it difficult to assess the extent to which tree diversity influences meiofaunal diversity. Gee and Somerfield (1997) found no strong differences in meiofaunal communities between sediments underlying stands of *Rhizophora apiculata* and *Bruguiera parviflora* in otherwise similar areas of the Merbok mangrove forest, Malaysia. Such differences as were detected were attributed to differences in tree root structure, the degree of disturbance by macrofauna, and the physical and chemical nature of the leaves falling to the sediment surface. It appears that the presence or absence of mangrove vegetation is relatively unimportant in determining the composition of meiofaunal communities.

It has been suggested that high levels of sediment-associated tannins in mangrove sediments reduce the abundance of meiofauna (Alongi, 1987c) but mangrove leaves that fall onto the sediment are rapidly colonised, and there is a succession of species associated with their decomposition (Schrijvers et al., 1995; Gee and Somerfield, 1997; Somerfield et al., 1998; Zhou, 2001). Such observations support the view that meiofauna play an important role in litter degradation. Another important ecological role of meiofaunal organisms in mangroves is that they are an important component of the diet of commercially important fish (Coull et al., 1995) and crustaceans (Dittel et al., 1997). Despite their abundance and ubiquity, however, detailed knowledge of the taxonomy, biology and interactions of these animals, and their role in the functioning of mangrove ecosystems, is lacking.

4. Mangroves as habitats for macrofauna

Mangroves are inhabited by a variety of benthic invertebrates, such as brachyuran crabs, gastropods, bivalves, hermit crabs, barnacles, sponges, tunicates, polychaetes and sipunculids. Mangrove invertebrates often show marked zonation patterns, and colonise a variety of specific micro-environments. While some species dwell on the sediment surface or reside in burrows, others live on pneumatophores and lower tree trunks or prop-roots, burrow in decaying wood, or can even be found in the tree canopies (Sasekumar, 1974; Ashton, 1999). The burrowing activities of certain benthic invertebrates have a pronounced effect on sediment properties and biochemical processes, by enhancing the porosity and water flow through the sediment, assisting in flushing toxic substances. In addition, their feeding on the sediment surface (deposit feeding) and plant matter (detritivory) promotes nutrient recycling (see also Kristensen et al., 2008). In turn, benthic invertebrates are a source of food for vertebrate predators including shallow-water fishes that enter the mangroves at high tide (Sheaves and Molony, 2000).

Macrobenthos may be operationally separated in two groups, i.e., epifauna and infauna. Epifauna refers to those invertebrates that live on various substrates such as lower tree trunks and the sediment surface, but which do not burrow in it. A range of gastropods, crabs, and bivalve species are typical representatives of epifauna. Infauna refers to burrowing invertebrates which live within the sediment, and includes crabs, pistol prawns, polychaetes, and sipunculids. The distinction between infauna and epifauna is not always straightforward, however, and not always related to the organisms' functional role. For example, while many sesarmid crabs create extensive burrow systems, others appear to find refuge in crevices from decaying wood or root structures, or their burrowing status is unknown (see Gillikin and Kamanu, 2005).

4.1. *Diversity and distribution of macrofauna*

Macrofaunal communities in high and low intertidal mangroves are often distinctly different, and this relates in part to highly different environmental conditions. They appear to be influenced by hydroperiod, availability of organic matter and sediment characteristics (Lee, 2008). Lower intertidal mangrove sediments (typically silt- or clay-dominated) provide substratum for growth of benthic microalgae and macroalgae (Dor and Levy, 1984; King and Wheeler, 1985; Tanaka and Chihara, 1988; Aikanathan and Sasekumar, 1994; Sarpedonti and Sasekumar, 1996). In high intertidal mangroves, the substratum is often more sandy, and the reduced frequency of tidal inundation results in a drier, more saline environment where more leaf litter accumulates and which is less suitable for growth of micro- and macroalgae. Frequent inundation in the low intertidal zone also favours the presence of filter feeders and deposit feeders, whereas fauna in the high intertidal zone does not have frequent direct access to such food sources and other trophic groups therefore predominate there.

Gastropods are typically one of the dominant and most conspicuous macrofauna in mangrove systems, and occupy a wide range of ecological niches (Cantera et al., 1983; Plaziat, 1984). The distribution of gastropod species within a mangrove forest is influenced by a variety of factors such as light (as a major factor determining algal growth and as a factor influencing humidity), tidal exposure, salinity, and substrate type. The trophic position of gastropods is equally varied (see also Section 9): sediment dwellers feed – selectively or not – on sediment organic matter and/or microphytobenthos, *Littoraria* spp. feed on epibenthic crusts on stems and roots, and some species have been reported to feed on mangrove litter and/or propagules (such as *Melampus coffeus* and adult *Terebralia palustris*). Predatory and scavenging species such as *Thais* spp. and *Nassarius* spp. are much less abundant. Gastropods can attain very high species diversity in some mangrove ecosystems: Camilleri (1992) mentions 39 species of gastropods in an Australian mangrove, Jiang and Li (1995) found 28 species in a Chinese mangrove, and Wells (1990) reports 23 mollusc species from a mangrove forest in Hong Kong. On the other hand, species diversity differs strongly in different parts of the world, e.g., *M. coffeus* is the only gastropod present in the mangroves of Guadeloupe (Plaziat, 1984). The numerical abundance and biomass of molluscs can be equally impressive (e.g., Sasekumar, 1974), and they can even reach higher densities and biomass than brachyuran crabs in some cases (e.g., Wells, 1984), although the number of comparative studies is limited. A number of gastropod genera (e.g., *Ellobium*, *Enigmonia*) and species (e.g., *Littoraria scabra*, *T. palustris*) appear to occur exclusively in mangrove systems (Plaziat, 1984). The global pattern in species richness of mangrove gastropods closely follows that of mangrove trees (Ellison et al., 1999).

Bivalves are often considered to be confined to a narrow seaward zone, due to feeding and larval settlement restrictions (Plaziat, 1984). In Southeast Asia, however, *Polymesoda erosa* is adapted for a semi-terrestrial existence by living on the high shore where only occasional high tides inundate the habitat (Morton, 1976). A number of bivalves with chemo-symbiotic associations have also been reported from mangroves (e.g., Lebata and Primavera, 2001). Wood-boring bivalves are also common in the mangrove forest, and Singh and Sasekumar (1994), for example, reported 10 species of teredinids and 1 pholadid in several mangroves along the west coast of Peninsular Malaysia. These wood-boring bivalves are ecologically significant as they stimulate the decomposition of wood and live in symbiosis with nitrogen-fixing bacteria (Waterbury et al., 1983). It has been suggested that the latter process may represent a very significant yet overlooked source of nitrogen fixation in mangrove ecosystems in view of the abundance of dead wood and Teredinidae (Boto and Robertson, 1990). Although mangrove-associated bivalves are only rarely studied, their diversity can be surprisingly high: Alvarez-Leon (1983) reported 29 species of bivalves from the mangrove root systems on the Atlantic coast of Colombia, and Jiang and Li (1995) mention 24 bivalve species from a mangrove system in Hong Kong.

Together with molluscs, brachyuran crabs are the dominant macrofauna in most intertidal mangrove ecosystems. Early reports on the species diversity of mangrove-associated crabs in the Indo-Pacific (Jones, 1984) now appear to be outdated (see Lee, 1998), and as taxonomical difficulties are still a major restriction, the diversity and distribution of mangrove-associated crabs is likely to be far from understood. Ocypodid crabs (*Uca* spp. and *Macrophthalmus* spp., or *Ucides cordatus* in Central and South American mangroves) and grapsid crabs (Sesarminae, *Metopograpsus* spp., *Metaplax* spp.) usually dominate the crab fauna and species often exhibit marked horizontal and vertical zonation patterns (e.g., Frith et al., 1979; Jones, 1984; Frusher et al., 1994; Sivasothi, 2000). Whether these distribution patterns are related to physico-chemical characteristics of the environment (e.g., Frusher et al., 1994), or to the presence of specific tree species or tree diversity, remains to be determined (see Lee, 1997; Dahdouh-Guebas et al., 2002). Similar to what is observed for gastropods (Ellison et al., 1999), species richness of sesarmid crabs appears to follow global patterns in mangrove tree species richness (Lee, 1998), although the number of detailed surveys is relatively limited and taxonomical problems still exist. Sesarmids are most diverse in Southeast Asia and decrease to low numbers in Central America. Only five species of Grapsidae have been found in the mangroves of Florida and Central America (Abele, 1992). However, Alvarez-Leon (1983) recorded an impressive array of Grapsidae (16 species) on the Caribbean coast of Colombia.

Other relatively well represented groups of macrofauna such as polychaetes and hermit crabs have been much less frequently studied, and little is known on their overall diversity, abundance and functional role in mangroves. Worms can attain a high diversity in the soft, unconsolidated substrates on the seaward sides of mangroves, with polychaetes predominating in diversity as well as abundance (Metcalfe and Glasby, in press).

4.2. Functional role of macrobenthos

The mangrove macrobenthos is intimately associated with the bottom substratum. Crabs and gastropods ingest sediment and food such as bacteria, microalgae, meiofauna and detritus adhering to it, they burrow in it and move through it, and modify it in many physical and chemical ways (e.g., Warren and Underwood, 1986; Smith et al., 1991). Crab burrows provide an efficient mechanism for exchanging water between the anoxic substrate and the overlying tidal water (Ridd, 1996). This observation was confirmed by Stieglitz et al. (2000) who demonstrated that a burrow inhabited by a sesarmid crab and a pistol prawn was completely flushed within 1 h by the activities of the crustaceans during a single tidal event.

Crabs and gastropods are the two major seed predators in mangrove forests, and thus play an important role in determining plant community structure (Smith et al., 1989). An inverse relationship between the dominance of a given tree species in the canopy and the amount of seed predation was found for species of *Avicennia*, *Rhizophora* and *Bruguiera*. It is apparent there is a mutual relationship between sesarmid crabs and mangroves, whereby mangroves provide a suitable habitat for the crabs, and the crabs reduces competition between mangrove plant species through selective predation on seedlings (Bosire et al., 2005). The selective effects of seed predation are not limited to sesarmid crabs, but can include land crabs and hermit crabs (Lindquist and Carroll, 2004). High seed predation by crabs can sometimes have a negative influence on regeneration of mangrove stands (Dahdouh-Guebas et al., 1997, 1998). Grapsid crabs dominate in Australia, Malaysia and Panama, while the gastropods *Cerithidea scalariformis* and *Melampus coeffeus* are the most important seed predators in Florida mangroves.

Detritus-feeding invertebrates dominate the mangrove fauna. *Ucides cordatus*, a semi-terrestrial ocypodid crab in Brazilian mangroves, feeds almost exclusively on plant material. Large male crabs consumed 3.3 g dry weight daily corresponding to 6% of their dry body weight (Nordhaus, 2004). Deposit feeders like *Uca* spp. scoop the surface layers of the sediment and derive nutrition from microalgae, bacteria and detritus. Some large sesarmid crabs are tree climbing and feed on fresh leaves (Sivasothi, 2000). Competition for mangrove litter has been observed in East African mangroves where many *Terebralia palustris* (potamidid gastropod) feed on the same leaf to prevent crabs from removing the leaf (Fratini et al., 2001).

The dominant role of grapsid crabs in the mangrove community structure and function has been investigated in Australia, Asia and East Africa (Giddens et al., 1986; Robertson and Daniel, 1989; Micheli, 1993; Lee, 1997; Ashton, 2002; Cannicci et al., 2008). The role of grapsid crabs as an agent affecting mangrove litter turnover in the Indo-Pacific is indisputable, but the exact trophic link remains unknown (Lee, 1997; see Section 9).

Numerous studies in Australia and East Africa indicate that grapsid crabs are major consumers of mangrove leaf litter and as a consequence produce large quantities of faecal material rich in nutrients and energy (Leh and Sasekumar, 1985; Micheli et al., 1991; Emmerson and McGwynne, 1992; Lee, 1997). These crabs also spend considerable time grazing and picking organic material off the surface of the substrate (Skov and Hartnoll, 2002), suggesting that they are using microbial resources for their nitrogen needs.

Fish predation on mangrove invertebrates occurs at high tide when the mangroves are inundated (Sasekumar et al., 1984; Wilson, 1989; Sheaves and Molony, 2000). For example, the mangrove crabs *Chiromantes* spp. and *Metaplax* spp., and the sipuncula *Phascolosoma arcuatum* were found in the gut of fishes that were netted within the mangroves at high tide (Sasekumar et al., 1984). To what extent this form of feeding contributes to the food of shallow-water fish community and controls the structure of the mangrove benthic community awaits further studies.

In summary, benthic invertebrates in mangrove forests play an important ecological role by their activities of burrowing in the sediment where they assist in flushing toxic substances, and modifying the oxidation status of the surrounding sediment. Feeding on plant matter (detritivory) assists in recycling organic matter and produces animal biomass which is a source of food for vertebrate predators (e.g., reptiles, birds, and otters) and inshore fishes that come in with the high tide.

5. Mangroves as habitats for prawns

Dall et al. (1990) classified penaeid prawn life cycles into four different types according to the environments in which the adults spawned and the postlarvae settled. Adults of two of these types both spawn offshore, and their larvae move inshore where the postlarvae settle in their preferred nursery grounds, either estuarine or nearshore habitats. The postlarvae develop into juveniles which spend between 6 and 20 weeks in the nursery ground before emigrating offshore (Haywood and Staples, 1993). The nursery grounds are generally dominated by some form of vegetation: either seagrasses (Coles and Lee Long, 1985), algae, mangroves (Staples et al., 1985), or saltmarshes (Webb and Kneib, 2002; Minello et al., 2003).

In one of the few comprehensive studies on epibenthic communities of mangroves, Daniel and Robertson (1990) found that, along with small fish, penaeids dominated the epibenthos. While a range of juvenile prawn species have been caught either within, or (more often) in the river or creek channels adjacent to, mangroves, only a few species have been found to be almost exclusively associated with mangroves as juveniles, e.g., *Penaeus*[1] *merguiensis* (Staples et al., 1985), *P. indicus* (Rönnbäck et al., 2002; Kenyon et al., 2004) and *P. penicillatus* (Chong et al., 1990). Other species are less specific in their choice of nursery habitat, e.g., *Metapenaeus ensis* (Staples et al., 1985), *M. monoceros* (Rönnbäck et al., 2002), *M. brevicornis* and *M. affinis* (Chong et al., 1990). In addition to being associated with mangroves they are also found in other habitats such as mud flats and seagrass beds.

Prawns can only gain access to intertidal mangrove forests for 10–12 h each day, when they are inundated by the tide. When the tide recedes the prawns move out, and in the case of *Penaeus merguiensis* and *P. indicus*, aggregate close to the water's edge (Staples, 1980; Kenyon et al., 2004). Because of the difficulty of sampling amongst the mangrove trunks, prop-roots and pneumatophores, most sampling for juvenile prawns (and other epibenthos) in mangrove habitats has been done using small beam trawls (Staples and Vance, 1979) or seines (Robertson, 1988) in the creek or river channels adjacent to the mangroves after the water has receded, or by setting trap nets on an ebbing tide across the small channels which drain the mangroves (Robertson, 1988; Robertson and Duke, 1990b). It is only relatively recently that researchers have examined the distribution of prawns and fishes within the mangrove forest using either drop samplers (Sheridan, 1992) or some form of stake- or lift-net to enclose an area of mangrove at high tide and collect the fish and epibenthos once the water has receded (Vance et al., 1996, 2002; Rönnbäck et al., 1999, 2002; Meager

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[1] The subgenera of *Penaeus* were elevated to genera by Pérez-Farfante and Kensley (1997). However, as there is some controversy over this revision we have chosen to use the old names in this paper (Lavery et al., 2004; W. Dall, CSIRO Marine and Atmospheric Research, personal communication).

et al., 2003). Prawns seem to make extensive use of the mangrove forest during high tide; in northern Australia, Vance et al. (1996) sampled mangroves at the creek fringe and at sites up to 59 m inland from the creek banks. Juvenile *P. merguiensis* appeared to distribute themselves throughout the forest as the tide rose, sometimes moving as far as 200 m into the mangroves (Vance et al., 2002). Similarly, working in the Philippines, Rönnbäck et al. (1999) found *P. indicus* and *Metapenaeus ensis* moved between 55 and 93 m from the mangrove fringe into the forest. In contrast, other studies have indicated that while *P. merguiensis*, *P. indicus* and *M. bennettae* move into the forest as the tide rises, densities are higher closer to the creek-mangrove interface (Rönnbäck et al., 2002; Vance et al., 2002; Meager et al., 2003). It is possible that these differences are due to variation in local topography between the study sites.

5.1. *Influence of abiotic factors on prawn distribution*

Many mangrove systems are located in estuaries and so are characterised by being subjected to a wide range of salinities. Juvenile prawns are euryhaline and so are able to cope with these fluctuations. Large postlarvae and juveniles of many species of penaeids are more tolerant of low salinities than early-stage postlarvae or adults (Dall, 1981). In fact, some authors have suggested that the postlarvae of certain species may use low salinity as a means of locating potential nursery grounds (Williams and Deubler, 1968; Hughes, 1969; Young and Carpenter, 1977), although high levels of rainfall (and presumably very low salinity) may inhibit postlarval immigration (Vance et al., 1998). Salinity fluctuations do no appear to significantly affect abundance, growth or mortality of penaeids (Staples, 1980; Haywood and Staples, 1993; Ahmad Adnan et al., 2002; Meager et al., 2003).

One of the main factors attributed to eliciting emigration of penaeids from mangroves out to sea is rainfall (Staples, 1980; Staples and Vance, 1986). Presumably the penaeids are responding to some other factor resulting from the increased rainfall, such as decreased salinity, increased current velocity, or changes in the levels of nutrients or other chemicals (Staples, 1980). Rainfall alone explained 70% of the observed variation in numbers of *Penaeus merguiensis* emigrating from the Norman River in northern Queensland, Australia (Staples and Vance, 1986). The amount of rainfall also determined the size at which the prawns emigrated; in very wet years a wide size range of prawns emigrated, whereas in relatively dry years only the larger prawns emigrated (Staples, 1980; Staples and Vance, 1986). In contrast to these results, studies on the closely related species *P. indicus* in South Africa indicated that emigration was related to temperature, although only temperature and salinity were recorded in this study and not rainfall (Benfield et al., 1990). Garcia and Le Reste (1981) noted that the relative importance of rainfall and temperature in determining emigration varies geographically. They postulated that in areas with a small temperature range, but seasonal rainfall, rain is the most important stimulus, whereas in areas that have rainfall that is extended throughout the year, change in temperature is more important.

Temperature has been shown to be positively related to the growth rate and negatively related to the mortality rate of juvenile *Penaeus merguiensis* in a tropical mangrove system in northern Australia (Haywood and Staples, 1993). Temperature has also been shown to influence penaeid catches in a temperate mangrove forest in Southeast Queensland, Australia. Meager et al. (2003) found that temperature was positively correlated there with catches of postlarval and juvenile *P. merguiensis*, although a long-term (6 years) study in tropical Queensland indicated that temperature explained very little of the variation in numbers of postlarval or juvenile *P. merguiensis* (Vance et al., 1998). Southeast Queensland is close to the southern limit of the distribution of *P. merguiensis*, and it is likely that the relationship with temperature found in the Meager et al. (2003) was because temperatures here ranged from 14 to 30 °C compared to 23.5 to 31.9 °C in the study by Vance et al. (1998).

Several studies have found higher densities of juvenile prawns, other crustaceans, and fishes in mangroves compared to adjacent nearshore habitats, and the hypotheses offered to explain this can be grouped into three general categories (Robertson and Duke, 1987; Robertson and Blaber, 1992; Chong, 1995; Manson et al., 2005): (1) that mangrove forests are more productive than alternative inshore habitats and so provide more food, (2) that the structural complexity provided by mangrove trunks, roots and debris, high turbidity and soft sediment afford greater protection from predators (Robertson and Duke, 1987), and (3) that the mangrove forest acts as a larval-retention mechanism, preventing planktonic prawn larvae from being distributed further by local currents (Chong et al., 1996). The remainder of this section will discuss the existing evidence for these hypotheses.

5.2. *Feeding*

There appears to be little doubt that juvenile prawns are foraging while they are inside the mangrove forests. Wassenberg and Hill (1993) collected samples of juvenile *Penaeus merguiensis* at various intervals during the tidal cycle and found that prawns had full guts as they left the mangrove forest on a receding tide, and inferred that the prawns had been feeding amongst the mangroves. An hour before low water, their guts were almost empty, indicating they had not been feeding after leaving the mangrove forest. Dietary studies have suggested that prawns eat a wide variety of food items including crustaceans, bivalves, gastropods, polychaetes, mangrove detritus, fish, insects, foraminiferans and diatoms (Chong and Sasekumar, 1981; Moriarty and Barclay, 1981; Leh and Sasekumar, 1984; Robertson, 1988; Wassenberg and Hill, 1993).

Because mangroves produce large amounts of detritus (Odum and Heald, 1975) it has been assumed that juvenile prawns and other mangrove-associated epibenthos have been able to utilise this production. However, although mangrove detritus has been identified in prawn guts (Chong and Sasekumar, 1981; Leh and Sasekumar, 1984; Robertson, 1988), cellulose is not digestible by penaeids (Omondi and Stark, 1996; Gonzalez-Pena et al., 2002) and so detritus, although ingested by penaeids, may not be assimilated (see Section 9).

5.3. Protection from predation

Predation is generally considered to be one of the key causes of mortality in prawns (Minello and Zimmerman, 1983; Robertson, 1988; Salini et al., 1998) and several studies have indicated that predatory fish consume significant numbers of juvenile prawns (Davis, 1985; Robertson and Duke, 1990b; Salini et al., 1990). Mangrove systems provide shallow water, structural complexity and in many cases high turbidity and fine sediment, suitable for burrowing prawns. These factors, in combination with the behaviour of prawns, acts to protect prawns by reducing their visibility to, and lowering their encounter rate with potential predators (Minello and Zimmerman, 1983; Laprise and Blaber, 1992; Kenyon et al., 1995).

Large predatory fish tend not to move far into the mangroves at high tide, whereas juvenile *Penaeus merguiensis* move long distances from the mangrove margin, making them less vulnerable to fish predation (Vance et al., 1996). The structural complexity provided by mangrove roots, trunks, detritus and fallen timber is thought to provide protection to juvenile prawns and other prey from fish predation (Robertson, 1988; Robertson and Blaber, 1992; Primavera, 1997; Meager et al., 2005). Protection from predation by mangrove structures is not as simple as might be expected; instead, it appears to be a complex interaction between predator species, prey behaviour and habitat complexity (Primavera, 1997; Meager et al., 2005). Primavera (1997) examined predation rates on two species of prawns, *P. merguiensis* and *P. monodon*, in laboratory experiments conducted on bare sand, coconut leaf bracts (to simulate mangrove detritus) and a range of different densities of pneumatophores. Two different species of predator (the barramundi *Lates calcarifer* and the mangrove jack *Lutjanus argentimaculatus*) were tested. Overall, significantly more prawns were eaten on the bare sand (48%) and leaf bracts (44%) than among the pneumatophores (30%). The presence of the structure (leaf bracts and pneumatophores) did not appear to affect the hunting abilities of the barramundi which chased prawns underneath the leaf bracts and between the pneumatophores, whereas the mangrove jack restricted themselves primarily to the clear water, away from the structure. Predation rates on *P. monodon* were lower on medium density pneumatophores compared to those on bare sand whereas there was no significant difference between predation rates on *P. merguiensis* on bare, medium or high-density pneumatophores. Primavera (1997) speculated that this may be due to behavioural differences between the two prawn species. The behaviour of prawns in relation to shelter may be modified by the presence of particular predators. Meager et al. (2005) noted that while juvenile *P. merguiensis* selected habitats providing vertical structure (pneumatophores or mangrove debris) over those with no vertical structure (bare substrate or leaf litter), once *L. calcarifer* was introduced to the tank, the prawns selected the mangrove debris over the pneumatophores. However, the prawns did not react to the presence of an alternative predator, the blue catfish *Arius graeffei*. Previous experiments had demonstrated that *L. calcarifer* was a more effective predator of juvenile *P. merguiensis* than *A. graeffei* (Meager, 2003).

High turbidity is a characteristic of many, but not all mangrove forests and turbidity within the mangrove forests may change dramatically depending upon the strength of tidal currents. While high turbidity may decrease the effectiveness of some prawn predators, others, particularly those using chemosensory mechanisms for prey detection, may be more successful in capturing prawns in turbid water (Minello et al., 1987; Macia et al., 2003).

5.4. Larval retention mechanism

The mouths of many mangrove-lined creeks are shallow and are characterised by extensive intertidal mud flats. The resulting high friction between the water and the mudflats means that, rather than forming tidal jets, the ebbing water spreads out in a fan-like manner at the mouths of the creeks (Wolanski et al., 1992). During periods of little or no longshore current most of the water from the swamp is returned during the following flood tide. In this way, mangrove swamps trap the lateral movement of coastal water for periods of between 2 and 8 weeks (Wolanski and Ridd, 1986; Wolanski et al., 1990) and so planktonic prawn and other larvae may be retained within the mangrove forest rather than being dispersed by currents (Chong, 1995). Even during the wet season water can be retained for weeks in the mangroves and side creeks (Robertson and Blaber, 1992). Lateral trapping is more effective in the upper reaches of a mangrove estuary than at the mouth (Wolanski and Ridd, 1986). This phenomenon may be responsible for influencing the along-river distribution of postlarval and juvenile *Penaeus merguiensis* observed by Vance et al. (1990). They found densities were almost five times higher in the upstream reaches of a small creek compared to those in the main river channel, near the mouth of the creek.

In summary, the fact that some species of juvenile prawns are found in relatively high densities within mangrove forests has been well documented, although the precise nature of the prawn–mangrove relationship is still unclear. There is a possibility that mangroves may be acting as a physical trap for water bodies containing the prawn larvae. While this seems plausible it does not explain why other species of prawns which have different habitat preferences (e.g., for seagrass) are not retained within mangroves as well. Based on the evidence available, mangroves seem to provide both food and protection from predation. Juvenile penaeids appear to be gaining their nutrients from mangrove-associated bacteria, epi- and infauna rather than directly from mangrove leaves or detritus.

6. Mangroves as habitats for insects

The global distribution of mangroves has been divided into two biogeographical hemispheres, the Indo-West Pacific and the Atlantic-East Pacific (Duke, 1992). The former ranges from the east coast of Africa to Asia, Australia and the western

Pacific islands, while the latter includes the eastern Pacific islands, the coasts of the American continent and the African west coast. Insect diversity in the mangroves of the Indo-West Pacific is thought to be higher than in the Atlantic-East Pacific as a result of higher plant diversity in the former although, to some extent, the dearth of insect species in the latter reflects gaps in our knowledge rather than low species diversity (Macintosh and Ashton, 2002). In general, the mangrove insect fauna of the Indo West Pacific has been better studied.

Mangroves provide a habitat that supports a large number of insects at different trophic levels. The primary trophic groups are (1) herbivorous insects that feed on leaves and other plant parts, (2) saproxylic and saprophagous insects that feed on dead and decaying organic matter, and (3) parasitic and predatory insects that feed or prey on other animals.

6.1. *Herbivorous insects*

Although the herbivorous insects of mangrove trees have sometimes been portrayed as being poor in diversity and lacking in specialists, more recent studies have shown that there is greater host specialisation and herbivory levels than previously thought (Burrows, 2003). In a study on herbivorous insects of mangroves in Singapore, Murphy (1990) found 102 herbivore species feeding on 21 species of mangrove plants from nine principle taxa. A wide range of mangrove plant parts were fed on, including leaves, shoots, flowers, fruits and stems. Stenophagy (feeding on narrow host range) appeared to be more developed among insects in *Avicennia* and *Sonneratia*, and was thought to be reflective of the relative taxonomic isolation of these plant taxa. In Queensland, Australia, little overlap was found between the insect herbivore fauna of *A. marina* and *Rhizophora stylosa*, and the diversity of herbivores on these tree species was similar to the diversity of nearby non-mangrove trees, and to the diversity levels reported for other tree species elsewhere in the tropics (Burrows, 2003). Mangrove habitat specificity has also been noted in a study on moths of the superfamily Geometroidea in Peninsular Malaysia, although species diversity in the mangrove habitat was low in comparison to that in other lowland forest types (Intachat et al., 2005). At the habitat level, however, mangroves can be expected to have lower herbivore diversity than other lowland forest types as a result of their lower plant diversity.

In butterflies, for which habitat and host associations are better known, few species are entirely restricted to mangroves (Corbet and Pendlebury, 1992). However, some butterfly species such as *Junonia* spp. (Nymphalidae) that occur in landward edge zones of mangroves and upper reaches of estuaries have host plants that are primary colonisers. These plants may be rare or absent under the closed multi-storey canopies of inland forests, but are able to persist in more open coastal habitats. The significance of these populations in natural coastal habitats is rarely recognised because many of the species are also able to colonise disturbed and man-made habitats such as parks and gardens. The few mangrove-inhabiting butterflies that occur across a range of natural habitats are oligophagous or polyphagous species such as *Hypolycaena erylus* (Lycaenidae) and *Polyura schreiber* (Nymphalidae) that have been recorded feeding on one or more mangrove plant species (Murphy, 1990), but feed on other non-mangrove host plants as well (Corbet and Pendlebury, 1992). A notable example of a monophagous mangrove specialist butterfly is *Danaus affinis* (Nymphalidae). The larvae feed on the vine *Ischnostemma selangorica* (Asclepiadaceae) that grows in the landward edge zones of mangroves, and the adults feed on nectar only from the flowers of the coastal shrub *Wedelia biflora* (Kirton and Azmi, 1996, 2000, 2004).

Special adaptations to the mangrove environment occur in a number of taxa of herbivorous moths. Moths of the pyralid subfamily Nymphulinae have aquatic larvae that feed selectively on the algae *Dictyota* (Dictyotaceae) and *Murayella* (Rhodomelaceae) in the intertidal zones of the mangrove floor (Yoshiyasu, 1984; Murphy, 1989). *Eristena mangalis*, a moth of the family Pyralidae, has aquatic larvae that feed on brown algae. The larvae have breathing filaments on the body, and build tube-like shelters in drainage channels under rotting leaves (Ng and Sivasothi, 2002). Other moths, such as *Cleora injectaria* (Geometridae), *Aucha velans* and *A. velliana* (Noctuidae), feed on the leaves of mangrove trees but pupate in the intertidal zone under rotting vegetation or algal mats at the base of their host plants (Murphy, 1990). A leaf-tying caterpillar of the moth genus *Argyroploce* (Tortricidae) has also been reported feeding on the tidally inundated leaves of young *Sonneratia griffithii* in Peninsular Malaysia, and was able to survive submersion in seawater for 4.5 h (Lever, 1952).

6.2. *Saproxylic and saprophagous insects*

Insects that feed on dead trees or wood (saproxylic insects) or decaying organic material (saprophagous insects) play an important role in nutrient cycling in forests. Termites and wood-borers (usually the larvae of beetles or moths) form the majority of saproxylic insects, and a relatively characteristic assemblage occurs in mangroves. The relative abundance of a limited number of tree species provides an abundant and stable food source for this group of insects.

In the intertidal zone, periodic or continuous flooding makes mangroves uninhabitable for many termite species that forage from the ground. However, species that nest above the ground thrive in this habitat in the absence of competing fauna and in the presence of abundant food resources. Among these are drywood termites such as *Glyptotermes*, *Neotermes* and *Cryptotermes*, which feed on dead branches that die in the canopy, or on dead standing trees (e.g., Miller and Paton, 1983; Salick and Tho, 1984). Their ability to feed on relatively dry wood is thought to be a result of an ability to obtain metabolic water through physiological processes in their bodies, as well as a result of structural adaptations that enable them to conserve water (Collins, 1969). The uniform, single-tiered canopy of mangrove forests results in a relatively low humidity in the canopy. Trees that die or branches that die in the canopy dry faster than in the multi-storied canopies of inland forests. Other termite groups that readily colonise the mangrove habitat are *Prorhinotermes* (Tho, 1992) and some species of *Coptotermes*

(Kirton, 1995), which are able to nest in moist wood with no ground contact, and species that build arboreal carton nests on tree trunks and branches, such as *Microcerotermes* spp. and some members of the subfamily Nasutitermitinae (L.G. Kirton, personal observations).

Scolytids and platypodids are the primary wood-boring beetles in mangroves. The majority feed on dead branches that have yet to dry completely. They burrow under the bark or into the wood and culture fungi on which their brood feeds. However, some are seed or prop-root feeders (Ng and Sivasothi, 2002), and others may cause the death of branches and trees through girdling and hollowing of stems and twigs. Their effects on some mangrove communities are known to exceed that of herbivores (Feller and Mathis, 1997; Feller, 2002).

A large number of ground-dwelling saprophagous insects can also be found in the mangrove habitat, and many have specialised adaptations for survival in the intertidal zone. Collembola (springtails) are diverse among the roots of mangrove plants and in the leaf litter that accumulates on the ground (Murphy, 1965; Roque, 2007), where they feed on a range of organic material including detritus and fungi. *Pseudanurida billitonensis* (Neanuridae) is a springtail in the mangroves of Singapore that feeds at low tide and returns to underwater shelters during high tide (Ng and Sivasothi, 2002). A pyralid moth, *Hymenoptychis sordida*, is known to feed on fallen fruit of *Avicennia*, dead leaves, roots and rotting timber on the mangrove floor in Singapore (Ng and Sivasothi, 2002). The larvae shelter in silken tunnels when the tide rises.

6.3. Parasitic and predatory insects

A wide range of predatory and parasitic insects with a great diversity of host and habit occur in mangrove habitats. These include predatory larvae and adult insects that prey on other organisms, parasitoids that feed within a single host and eventually kill it, hyperparasitoids that parasitize parasitoids, and blood-sucking parasites of vertebrates. They occur throughout the mangroves, from the soil to the water surface and on mangrove plants, where they exert a restraining influence on populations of herbivorous and saprophagous organisms.

Ants (Formicidae) are important predators in mangroves. One species of weaver ant, *Oecophylla smaragdina*, that is common in mangroves in Australasia, nests by drawing the leaves of mangrove plants together with silk threads spun by their larvae. The ant has been shown to significantly reduce herbivory levels on the mangrove tree *Rhizophora mucronata* in Thailand (Offenberg et al., 2004a), and the presence of this ant's pheromones on leaves of *R. mucronata* have been shown to deter feeding by the leaf beetle, *Rhyparida wallacei* (Chrysomelidae) (Offenberg et al., 2004b).

The best-known predatory insects that characterise the mangrove habitat are, arguably, fireflies (Coleoptera: Lampyridae). Although fireflies occur in a range of habitats, some are associated with mangroves and mangrove estuaries, where their larvae prey on snails in the intertidal zones. These include species of *Pteroptyx*, which range from South and Southeast Asia to New Guinea (Ballantyne and McLean, 1970; Ballantyne, 1987), and are well known for their impressive group displays on certain trees (Buck and Buck, 1976; Nallakumar, 1999; Zaidi and Yong, 2004). In Southeast Asia, members of groups of *Pteroptyx tener* or *P. malaccae* flash in close synchrony (Buck and Buck, 1976; Hanson, 1978). The synchronous flashes have made sites with large congregations of fireflies ecotourism destinations in some countries such as Malaysia (Nallakumar, 1999). *Pteroptyx tener* is the species for which the biology and ecology has been better studied (e.g., Kumar, 1979; Motuyang, 1994; Rahmat, 1996; Nallakumar, 2002; Nada and Kirton, 2004), particularly in Kuala Selangor, Malaysia, where the adults display and mate on riverside trees, especially the mangrove tree *Sonneratia caseolaris*. The larvae prey primarily on the snail *Cyclotropis carinata* (Assimineidae) in tidally inundated areas of the riverbanks. They are able to enter the shells of the snails and inject a paralysing toxin and enzyme into the soft body tissues of the snails to aid in feeding.

Many other predatory insects live and feed on the ground, sheltering under plant debris during high tides and emerging to feed on springtails, copepods, protozoa and nematodes when the tides recede (Ng and Sivasothi, 2002). Among the more common are heimpterans and pselaphid beetles. On the water surface of mangrove tidal pools, water skaters (*Xenobates* sp., Veliidae) prey on smaller insects that fall or land on the water (Ng and Sivasothi, 2002).

Female mosquitoes (Culicidae) and other small biting flies (Ceratopogonidae, Simuliidae and Phlebotominae) that inhabit mangroves take a blood meal from vertebrate hosts prior to reproduction. Biting midges breed in the mud in mangroves and mosquitoes breed in stagnant pools as well as rot holes in trees. One species of mosquito in East Africa, *Aedes pembaensis*, is known to lay its eggs on the claws of the crab *Neosarmatium meinerti*, and the larvae develop in the burrow of the crab (see Hogarth, 1999).

7. Mangroves as habitats for elasmobranchs

The number of elasmobranch species recorded from fresh or estuarine waters is at least 171 species, representing 68 genera and 34 families, with the greatest diversity occurring along the rapidly developing tropical coastlines of South America, West Africa, and Southeast Asia. Of the 171 elasmobranch species, more than 50% occur in estuaries (Martin, 2005).

Estuaries are used by various species of euryhaline and obligate freshwater elasmobranchs, but their life history and ecology, including dependency on various habitats such as mangroves, is virtually unknown (Martin, 2005). Similarly, no information exists that compares the species diversity of rays versus sharks in mangrove habitats. Habitat selection by elasmobranchs is influenced by a multitude of interacting variables such as temperature, salinity, depth, substrate type, benthic vegetation, prey distribution and variability, predator distribution, social organisation, and reproductive activity (Simpfendorfer and Heupel, 2004). It is well known that many species of elasmobranchs rely on nearshore habitats as nursery grounds (Montoya and Thorson, 1982; Simpfendorfer and

Milward, 1993; White and Potter, 2004), with several species such as the nervous shark *Carcharhinus cautus* spending its entire life cycle in the estuaries of northern Australia (Lyle, 1987). However, separating the contribution of mangroves from that of the non-mangrove estuaries can be problematic as the functional roles of mangroves may be the same as those provided more generically by ‘estuarine’ and ‘nearshore’ environments (Loneragan et al., 2005). For example, estuaries without any mangroves can function as productive nursery habitats and thus the respective roles of estuary and mangroves may not be clear (Ruiz et al., 1993).

An acoustic telemetry study to determine habitat selection of juvenile lemon sharks (*Negaprion brevirostris*) at Bimini in the Bahamas, found that *Rhizophora* mangrove thickets were routinely selected according to their availability. The main abiotic factors influencing habitat selection were temperature, substrate type and depth (Morrissey and Gruber, 1993). It is well known that mangroves support large populations of prey on which elasmobranchs feed and also provide a complex habitat structure as a means of avoidance from large sharks and other marine predators (Robertson and Duke, 1987; Simpfendorfer and Milward, 1993). These biotic factors were considered to be the most likely to explain the use of mangrove habitat by *N. brevirostris* at Bimini (Morrissey and Gruber, 1993). In the large subtropical marine embayment of Shark Bay, Western Australia, mangrove tree density was found to influence the number of species and catch rates of elasmobranchs and their prey (White and Potter, 2004).

Within the shallow, nearshore waters of Shark Bay, the arid zone mangroves are considered particularly important feeding habitats for juvenile giant shovelnose rays (*Rhinobatos typus*) at high tide (White and Potter, 2004). In a comparable environmental setting in the remote, arid Exmouth Gulf of Western Australia, juvenile and neonate *R. typus* occur at a density of 3 m^{-2} within the fringing mangroves and salt flat habitats (H.M. Penrose, unpublished data). Due to fishing-related pressures, *R. typus* is listed on the IUCN Red List as ‘vulnerable’ to extinction on a global scale (IUCN, 2006). As with many other species of elasmobranch, clarification of the value of mangrove as habitat during this critical life history stage is fundamental for their conservation and management.

8. Mangroves as habitats for bony fishes

8.1. Diversity and distribution of fishes

The Indo-West Pacific region, stretching from the east coast of Africa through South and Southeast Asia to Australia and the Central Pacific, has the highest diversity of fishes in the world (at least 600 species in mangrove systems) (Blaber, 2000). The high diversity decreases latitudinally away from the equatorial *core area* (sensu Blaber, 2000) in Southeast Asia, but larger subtropical mangrove systems still contain at least 100 species. Many species occur throughout this region, while others are restricted to particular regions. Examples of species that occur in most mangrove areas of this region include the sly bream *Acanthopagrus berda*, the glassfish *Ambassis gymnocephalus*, the trevally *Caranx sexfasciatus*, the wolf herring *Chirocentrus dorab*, the tenpounder *Elops machnata*, the pursemouth *Gerres filamentosus*, the ponyfish *Leiognathus equulus*, the mangrove jack *Lutjanus argentimaculatus*, the flathead *Platycephalus indicus*, the flounder *Pseudorhombus arsius*, the whiting *Sillago sihama* and the thornfish *Terapon jarbua*. A special group of fish species found in mangroves are the mudskippers (family Periophthalmidae) which occupy a specialised niche in the intertidal zone. They are physiologically and morphologically adapted to an amphibious existence in this zone with highly variable environmental conditions (Clayton, 1993), and they are able to dwell on exposed mudflats when other fish species are forced to retreat to deeper waters with outgoing tides (Kruitwagen et al., 2007).

Mangroves occur in four tropical zoogeographic regions of the world (Indo-West Pacific, East Pacific, West Atlantic and East Atlantic) and the fish communities of all have many common characteristics. In almost all cases they are dominated by fishes of marine origin, with more than half the number of species as well as the number of individuals being contributed by either fully estuarine species or marine migrants. The mangroves of the tropical East Atlantic region along the west-African coast have somewhat fewer species than the Indo-West Pacific, but are still relatively rich, with larger estuaries such as the Senegal having more than 130 species, and smaller systems such as the Fatala in Guinea about 100 species. The tropical West Atlantic region from the Gulf of Mexico to northern South America has similar numbers of species, with most systems in the equatorial region containing at least 100 species.

The dominant taxa in each region are broadly similar, but there are some interesting contrasts. In all regions, except the Indo-West Pacific, Sciaenidae are one of the dominant families. In the Indo-West Pacific, sciaenids are important in the equatorial regions of Southeast Asia, but much less so elsewhere. This pattern may be connected with the amount of rainfall and the degree to which coastal waters approach estuarine conditions.

There are important differences in the relative proportions of freshwater species, both between and within regions. Freshwater species make up more of the fish fauna in tropical Atlantic mangrove systems than in the Indo-West Pacific or East Pacific, particularly in South America where many of the very diverse fauna of siluriid catfishes are common in estuaries (Barletta et al., 2005). Similarly, in West Africa various silurids and cichlids make a significant contribution to mangrove fish communities (Baran et al., 1999). In East Africa and Australia, however, freshwater species are usually insignificant components of the mangrove fish fauna (Blaber, 2000). The equatorial regions of Southeast Asia have somewhat more freshwater species than other areas of the Indo-West Pacific, but despite the diversity of the freshwater fish faunas of Borneo and Sumatra relatively few live in estuaries. Throughout the islands of the Caribbean most mangroves are non-estuarine and small in size (fringing), and typically contain marine species dominated by the families Gerreidae, Haemulidae, Lutjanidae and Scaridae (Rooker and Dennis, 1991; Acosta, 1997; Nagelkerken et al., 2000b).

One of the key influences of mangroves on fishes is the physical structure they provide. Their pneumatophores, prop-roots, trunks, fallen branches and leaves make a complex habitat for a host of potential prey organisms, and the rich epiflora of algae and diatoms found on the mangroves and associated substrata are an important food source for many fish species (Blaber, 2000; Verweij et al., 2006a). Because mangroves usually occur in shallow intertidal areas of deposition, with quiet waters, muddy substrata, variable turbidities and a rich fauna and flora, their effects on fish are inextricably linked with these factors. The whole suite of mangrove-associated biotic and abiotic conditions makes them one of the core fish habitats of tropical estuaries and lagoons (Blaber, 2007).

8.2. Influence of abiotic factors on fish communities

Almost all fishes living in subtropical and tropical mangroves are euryhaline and able to cope with salinities from almost freshwater (<1 ppt) to at least 35 ppt, but their ability to do so varies from species to species and hence may influence their distribution. Salinities down to about 25 ppt apparently pose few osmoregulatory problems for most tropical marine fishes. Salinities over vast areas of mangrove-fringed coastal waters in the tropics may decline in the wet season to as little as 20–25 ppt. In some areas, such as the Bay of Bengal and parts of the South China Sea, salinities seldom rise above 30 ppt and the fish communities of such areas are highly diverse (Pauly, 1985). Salinity is not only relevant to the distribution patterns and survival of fishes in estuaries, but may also affect metabolic processes. Peterson et al. (1999) have demonstrated that there is the potential for fluctuations and spatial variability in salinity to cause significant variability in the short-term growth rates of at least one species in nursery areas. Long-term salinity variations may also affect the distribution and occurrence of fish species in estuaries. In various studies, catch rates of the most abundant species were most strongly correlated with long-term (months and years) salinity patterns (Sheaves, 1998; Barletta et al., 2005; Lugendo et al., 2007a). In the coastal lake Nhlange, part of the Kosi system of northern KwaZulu-Natal, South Africa, the changes in the fish fauna in response to gradual changes in salinity were a reduction in the diversity of marine species and an increase in numbers of individuals of a few freshwater species (Blaber and Cyrus, 1981). Nevertheless, even at salinities of 1 ppt or less the system still contained 23 estuarine or marine species.

Turbidity is one of the major factors influencing the distribution of juvenile fishes in subtropical and tropical mangrove systems. In a study of the fishes of Moreton Bay, a large estuarine embayment on the Queensland coast, Blaber and Blaber (1980) showed that variations in turbidity correlated with different distribution patterns of fish which could be divided into three categories: those tolerant of turbidity, those indifferent to turbidity (comparatively few), and those intolerant of turbidity. Most fishes in mangroves are tolerant of high turbidities.

8.3. Factors determining the attractiveness of mangroves for fishes

Three hypotheses, namely (1) reduced predation, (2) increased food supply, and (3) increased living space or shelter, have been suggested to explain the attractiveness of usually turbid mangrove areas, as juvenile-fish nurseries (Blaber, 2000). Predation on juvenile fishes in mangroves may be less, because turbid waters reduce the effectiveness of large visual fish predators (Blaber and Blaber, 1980; Cyrus and Blaber, 1987a), shallow waters exclude large fishes (Shulman, 1985), and structure such as seagrass or mangroves enables small fishes to hide from predators (Laegdsgaard and Johnson, 2001). Evidence supporting the turbidity hypothesis comes from comparisons of fish densities across a variety of coastal habitats which show that the abundances of certain species respond positively to increases in turbidity. Further evidence comes from observations of greater abundances of piscivorous species in the creeks of the Dampier mangroves of Northwest Australia that receive no run-off from the land, and thus have much clearer waters (Blaber et al., 1985). Evidence supporting this hypothesis also comes from estuarine systems in which there is little or no mangrove habitat (e.g., the St. Lucia system in South Africa; Cyrus and Blaber, 1987b). However, if fish are responding solely to turbidity, it is possible that mangrove vegetation has little effect on the dependence of fish on estuaries.

Both the quantity and types of food may differ between mangrove areas and adjacent waters (Nagelkerken et al., 2000b). Many of the foods available in sheltered mangrove waters are rare or absent in offshore waters, particularly detritus and microfauna and flora, as well as aquatic macrophytes and their epifauna and flora. The presence of mangroves in tropical estuaries increases the diversity and quantity of food available to juvenile fishes (Blaber, 1980, 1987), and Robertson and Duke (1987, 1990a) have shown highly significant differences in the densities of juvenile fishes between mangrove and other nearshore habitats when they are immediately adjacent to each other. Furthermore, densities of zooplankton in mangrove habitats are greater (by an order of magnitude) during the late dry- to mid-wet season recruitment period of fishes, than in the middle of the dry season. Most newly recruited fish in estuarine or mangrove habitats are zooplanktivores. In intertidal mangroves, fishes typically enter the mangroves at high tide to feed (Vance et al., 1996; Sheaves and Molony, 2000; Lugendo et al., 2006). On Caribbean islands where mangroves are often permanently inundated, on the other hand, fishes mainly shelter in the mangroves during daytime and feed on adjacent seagrass beds at night (Nagelkerken et al., 2000a; Nagelkerken and van der Velde, 2004a). Nevertheless, opportunistic feeding takes place while they shelter in mangroves during daytime (Nagelkerken and van der Velde, 2004b; Verweij et al., 2006b).

The structural significance of mangroves for fishes is well demonstrated by the studies of Thayer et al. (1987) in Florida, Blaber and Milton (1990) in the Solomon Island, Vance et al. (1996) in Australia, and Rönnbäck et al. (1999) in the

Philippines. They showed that the prop-root habitat of mangroves is of major importance to a wide variety of fishes and that the species composition of fishes varies according to the species of mangrove tree, whether the channels are blocked or choked by fallen mangrove tree branches, and the type of substratum. Cocheret de la Morinière et al. (2004) showed in an experimental setup that different densities of prop-root mimics and different degrees of shading (mimicking the above-water mangrove canopy) affected the abundance of fish sheltering in them. It appears that mangrove-associated species inhabit mangrove prop-roots in higher densities than reef-associated species, because their juveniles occur more commonly in shallow-water mangrove areas and not because they possess a greater competitive advantage for mangroves compared the reef-associated species (Nagelkerken and Faunce, 2007). The importance of presence of mangrove-root structure is also shown by the positive effects on abundance and presence of fauna (e.g., crabs, fish, infauna) as a result of mangrove replanting (Bosire et al., 2004; Crona and Rönnbäck, 2005; Walton et al., 2007; Bosire et al., 2008).

The effects of differing structure are illustrated by reference to the physical characteristics of Solomon Islands estuaries, which are similar to those of other tropical Indo-West Pacific estuaries in terms of their salinity, temperature and turbidity regimes (Blaber, 1980; Blaber et al., 1989). There are two different types of mangrove estuaries in the Solomon Islands, based on substrata and mangrove tree species, each with a different fish fauna. Hard substratum estuaries with an abundance of mangrove tree debris are inhabited mainly by species that apparently need the cover or structure provided by the debris, such as Pomacentridae and some species of Apogonidae, together with juvenile Lutjanidae and Serranidae. These species are largely absent from the soft substratum estuaries that have little debris cover, where Gobiidae, including burrowing species are dominant.

The complexity of the interplay among various factors on the distribution of fishes in mangroves is exemplified by the study of Rönnbäck et al. (1999) who showed that the numbers and biomass of fish species were higher among the pneumatophores than in the prop-root areas in Philippine mangroves. This was thought to be because the limited height of pneumatophores allows a larger volume of water free of roots where fish can swim without encountering structural complexity. Also food items associated with mangroves are much more concentrated among pneumatophores compared to among the relatively less dense prop-roots, thereby facilitating feeding (Rönnbäck et al., 1999). For both root types, the densities of small fishes were higher and that of larger carnivores lower than in more seaward habitats. Verweij et al. (2006a) showed that some species mainly utilised prop-roots for shelter whereas other species mainly used them for feeding.

In summary, the three hypotheses of predator avoidance, food and shelter, are probably all important. However, their relative significance, in terms of dependency and utilisation of tropical and subtropical mangroves by fishes, will vary depending upon the fishes and the nature of each system and its mangroves (Pittman et al., 2004; Sheridan and Hays, 2003; Lugendo et al., 2006).

9. The role of litter in the mangrove food web

9.1. Importance of mangrove litter

The idea that mangroves provide a trophic link with the abundant faunal communities within the mangrove ecosystem and in adjacent habitats has been a longstanding issue in the literature and was first proposed by the classical work of Odum and Heald (1972) in their ‘outwelling hypothesis’. Odum and Heald suggested that the high productivity of mangroves is partially exported to the aquatic environment, providing an important food source for secondary consumers and thereby supporting adjacent fisheries. It has become increasingly apparent over the past two decades that this hypothesis needs to be revised, since a number of studies using natural tracer techniques (e.g., stable isotopes, fatty acids) have almost invariably found little solid evidence for a significant amount of mangrove-derived carbon in adjacent food webs, and that many of the earlier estimates may have been biased and should be revised (see Bouillon et al., 2008, for a recent overview). Relationships between fisheries or shrimp catch and the presence or extent of nearby mangroves are therefore unlikely to result from a direct trophic link, but rather from the effects of other factors such as the provision of a suitable nursery habitat, refuge from predators, or the provision of other food sources besides mangrove litter (see Sections 5, 8, and 10). The contribution of mangrove-derived organic matter in adjacent systems also appears to vary according to the environmental setting and geomorphology of the system, being more important in riverine/estuarine systems than in lagoon or island settings (Pineda, 2003).

Despite the evidence that mangroves are far less important as a food source for aquatic faunal communities than previously assumed, the assumption that they sustain intertidal food webs has endured much longer, and is often taken for granted. A number of prominent mangrove-dwelling species are indeed known to remove and consume leaf litter, in particular sesarmid crabs (e.g., Lee, 1998) and species such as the crab *Ucides cordatus* (Nordhaus et al., 2005) and the gastropod *Terebralia palustris* (Slim et al., 1997). Subsequently, there is a wealth of literature on the impact of mangrove invertebrates on litter dynamics, and on feeding experiments involving various species of mangrove tree leaves or their state of senescence (see Lee, 1998, for references). The amount of literature exploring the trophic importance of other primary producers, in contrast, is far more limited. The general view emerging from recent studies is that, although faunal communities may have a profound impact on litter dynamics (Lee, 1998; Kristensen et al., 2008), the role of mangrove litter in sustaining epibenthic communities is often fairly limited, and decreases when systems are more open with respect to material exchange with adjacent systems (Bouillon et al., 2004).

9.2. Importance of other carbon sources

When a variety of food sources are available, mangrove fauna show a remarkable diversity in their resource utilisation patterns of the different sources, with different faunal groups each occupying a different trophic niche (Bouillon et al., 2002). Sesarmid crabs, considered to be key consumers of fallen litter, generally show the highest degree of dependency on mangrove carbon in comparison to other faunal taxa. However, in systems where other inputs are considerable, certain species, and in particular juveniles, show a high reliance on imported material and microphytobenthos (Bouillon et al., 2004). Moreover, several studies have indicated that mangrove litter alone would not suffice to meet the nitrogen requirements of sesarmids (Skov and Hartnoll, 2002; Thongtham and Kristensen, 2005). In contrast to sesarmids, fiddler crabs (*Uca* spp.) which are also typically highly abundant in mangrove systems rely mainly on microphytobenthos (France, 1998; Meziane et al., 2002). Other important groups of brachyuran crabs in mangrove systems are known to feed to an important extent on macroalgae (e.g., certain *Metapograpsus* spp.: Dahdouh-Guebas et al., 1999) or forage on other fauna (e.g., *Epixanthus* spp., *Scylla* spp.: Dahdouh-Guebas et al., 1999; Bouillon et al., 2004). Molluscs constitute the second major group of mangrove epifauna, and show equally diverse feeding preferences. This includes grazing on epiphytic algae on tree trunks or pneumatophores (e.g., *Onchidium* spp. and *Littoraria* spp.: Christensen et al., 2001; Lee et al., 2001; Bouillon et al., 2004), utilising surface organic matter and microphytobenthos (e.g., *Assiminea* spp. and *Cerithidea* spp.: Bouillon et al., 2004), selective or unselective filter-feeding on suspended matter (for a number of bivalves: Bouillon et al., 2004), and consuming mangrove leaf or propagule litter (*M. coffeus*: Proffitt and Devlin, 2005). In addition, some molluscs have particular adaptations, such as wood-boring shipworms (*Teredinidae*) which harbour symbiotic bacteria capable of N_2 fixation to supplement their N-poor diet (see Bouillon et al., 2002), and sacoglossan seaslugs, some of which retain functional chloroplasts from their food algae ('kleptoplasty': see Bouillon et al., 2008). Previous studies have likely been biased towards more conspicuous groups of fauna, with much less attention to infauna and meiofauna, where recent results suggest that a variety of chemo-symbiotic relationships exist in reduced mangrove sediments (see Bouillon et al., 2008). An integrated view of the importance of different primary sources for consumers, or of the quantitative impact of mangrove fauna on material processing, is still lacking, due to the absence of solid combined datasets on feeding preferences and secondary production or consumption rates. Moreover, there is likely no general 'mangrove food web' and the importance of various sources and the impact of fauna on organic matter turnover will significantly depend on the environmental settings and the faunal community composition.

A number of exclusion/inclusion experiments carried out in mangrove systems demonstrate that the presence and activity of macro-epifauna (e.g., gastropods, ocypodid crabs) cause a significant modification of the benthic habitat. The exclusion of fauna may increase the micro-epiphytic biomass due to the absence of grazing (Branch and Branch, 1980; Kristensen and Alongi, 2006) and indirectly cause a modification of meiofaunal communities (Schrijvers and Vincx, 1997; Schrijvers et al., 1998; Carlén and Ólafsson, 2002). Such studies are scarce for mangrove systems, but offer a valuable alternative perspective on trophic interactions and on the mechanisms structuring mangrove faunal communities.

9.3. Linkages with adjacent systems

An important issue in the ecological and habitat function of mangroves is the importance of mangrove areas as feeding habitats for mobile or visiting fauna (Fry and Ewel, 2003). A number of studies suggest that mangroves can provide an important feeding habitat for foraging fish or prawns during high tide, based on observational evidence, gut content analyses, and stable isotope evidence.

For certain mangrove fish species, the importance of predation on mangrove food sources, such as sesarmids and other invertebrates, has been indicated by a number of studies (e.g., Sasekumar et al., 1984; Thong and Sasekumar, 1984; Wilson, 1989; Sheaves and Molony, 2000; Lugendo et al., 2006). The accessibility of the intertidal zone and its potential role as a refuge or feeding habitat is constrained by the tidal regime and system characteristics (Sheaves, 2005; Lugendo et al., 2007b). Lugendo et al. (2007b) showed that feeding by fishes within mangroves is more common when they are permanently accessible than when they are only temporarily accessible due to the tidal regime. Nagelkerken and van der Velde (2004a) and Verweij et al. (2006b) demonstrated that the majority of fish species from a Caribbean mangrove–seagrass–reef system derived little or no food from the mangrove habitat, even though they were permanently inundated, which is consistent with the relatively low tidal amplitude in this region. A probable cause is that Caribbean island mangroves are narrow fringes which provide excellent shelter habitat but little food (Nagelkerken et al., 2000a). As a result, fish that shelter there during the daytime migrate to adjacent seagrass beds at night for most of their feeding activities, while the same species sheltering in seagrass beds derive their food entirely from within that habitat (Nagelkerken and van der Velde, 2004b; Nagelkerken et al., 2006).

9.4. Modelling mangrove food webs

The lack of basic data on the origin of organic matter sustaining different faunal communities is also propagated in modelling approaches to describe the food web structure and energy flows in mangrove systems. A number of studies (e.g., Manickchand-Heileman et al., 1998; Ray et al., 2000; Wolff et al., 2000; Vega-Cendejas and Arreguín-Sánchez, 2001) have used a network analysis approach, typically using Ecopath software (Christensen and Pauly, 1992) to construct an integrated view on energy flow in mangrove systems. While this approach has its own merits and, moreover, has the potential to be an excellent tool to estimate the potential effects of ecosystem changes on overall energy flow, the input data for such models require solid knowledge on the feeding habits of critical ecosystem components. It is worth noting that, while recent studies stress the importance of microphytobenthos and allochtonous carbon sources to intertidal food webs, current models (cited earlier) have not included microphytobenthos in their analyses. The assumption that mangrove litter or mangrove-derived detritus represents the dominant food source for certain major groups of fauna (e.g., fiddler crabs; Wolff et al., 2000) is likely to significantly bias model output, since tracer studies indicate that mangrove-derived carbon contributes only marginally to these organisms' diets (e.g., France, 1998; Meziane et al., 2002; Bouillon et al., 2004). Such bias is inevitably transferred to higher trophic levels. In this context, there is clearly a need for more synergy between specific tracer studies, experimental field studies on trophic interactions, and trophic models in order for these modelling efforts to generate more realistic outputs, and for results from other approaches to generate more added value.

10. Mangroves as drivers of nearshore fishery production

10.1. The role of mangroves and estuaries in relation to fisheries

Over the last four decades, many studies have demonstrated a strong relationship between mangrove presence and fish catch (Turner, 1977; Yáñez-Arancibia, 1985; Pauly and Ingles, 1986; Lee, 2004; Manson et al., 2005; Meynecke et al., 2007), with fishery catch being influenced by the relative abundance of mangroves in a region. Correlations have also been found between the extent (area or linear extent) of mangroves and the catches of prawns (particularly banana prawns) in the fisheries adjacent to the mangroves (Turner, 1977; Staples et al., 1985; Pauly and Ingles, 1986; reviewed in Baran, 1999). Such studies provided important information on the fisheries–mangrove relationship and were the base for economic valuation of mangroves (e.g., Barbier and Strand, 1998; Grasso, 1998; Barbier, 2000). This observed relationship mainly derives from a group of economically important species classified as estuarine-dependent (Cappo et al., 1998) or (non-estuarine) bay-habitat-dependent (Nagelkerken and van der Velde, 2002). Mangroves, or similar environments, are the principal habitat for at least one part of their life cycle (Blaber et al., 1989; Nagelkerken et al., 2000b). Typically, the adults spawn offshore, producing eggs that disperse in the water column for varying lengths of time. The eggs then develop into planktonic larvae which move, or are carried by currents, into inshore and estuarine waters. The subadults or adults migrate out of the estuary or lagoon, and back towards the offshore areas or adjacent coral reefs. Therefore, mangroves could function as an important link in the chain of habitats that provide complementary resources and benefits, e.g., as nursery areas for fish, prawns and crabs (Sheridan and Hays, 2003; Crona and Rönnbäck, 2005), with spatial complexity at a scale that provides refuge to small prey, and abundant food for commercial species at certain stages in their life cycle (Chong et al., 1990).

10.2. Controversy in the literature: nursery ground and outwelling

Opinions vary as to the importance of mangrove habitats to fish and, by extension, to nearshore fisheries (Blaber et al., 1989; Thollot, 1992). Although, studies have documented greater abundances of juvenile species in mangroves than in other estuarine and inshore habitats (Robertson and Duke, 1990a; Nagelkerken and van der Velde, 2002), other studies found a significant contribution by saltmarshes (Connolly, 1999). Controversy also surrounds the measurement of nursery ground values (Sheridan and Hays, 2003). Beck et al. (2001) and Adams et al. (2006) gave a detailed discussion of the nursery habitat concept, where the value of nursery grounds is measured in terms of numbers contributed to adult populations: either the average number of individuals per unit area (Beck et al., 2001) or the total number of individuals per habitat (Dahlgren et al., 2006; see also Layman et al., 2006), in an attempt to simplify the measurement of nursery function and to identify core components (e.g., habitats) that are most important in maintaining overall ecosystem function. Sheaves et al. (2006) argued that this approach is oversimplistic and relates to the value of a nursery from a short-term, fisheries perspective. It is important to develop a better understanding of habitat connection and how these connections can be maintained (Meynecke et al., 2007).

The discussion about the importance of tidal wetlands for fisheries includes the debate on the passive transport of dissolved and particulate nutrients and detritus from productive tidal wetlands to coastal and offshore waters, termed 'outwelling'. Outwelling was considered critical in supporting the secondary production of many coastal fisheries (Nixon, 1980). The transport of nutrients between estuarine and coastal systems is now recognised as a complex and dynamic process (Ford et al., 2005; Webster et al., 2005), and the general model of outwelling appears too simplistic (Kneib, 1997; Ford et al., 2005; see also Section 9). Recent studies using stable isotope analysis and other trophic tracers indicated that offshore fisheries may not be driven through the outwelling of nutrients from estuaries (Loneragan et al., 1997; Connolly, 1999; Chong et al., 2001; Melville and Connolly, 2003) and that, for example, mangrove-derived nutrients only contribute directly to the food webs of some animals within highly restricted areas, e.g., mangrove-lined creeks (Loneragan et al., 1997). Separating the contribution from mangroves, seagrass and salt marshes using casually deployed tracers, such as natural abundance stable isotope analysis, is still problematic since benthic and pelagic organisms seem to rely on different mixes of organic matter sources.

10.3. Studies linking fish catches with mangroves and estuaries

The most direct approach to search for links between mangroves and fisheries is to use fish catch data in comparison with mangrove or estuarine parameters. Manson et al. (2005) found a significant influence of mangrove forest characteristics (e.g., perimeter and area) on mangrove-related and estuarine fishery species, while latitude was the only variable influencing catch of offshore species along the north-eastern Australian coast. The earliest studies in this field were completed by Macnae (1974) who showed that inshore fish production in Malaysia was related to mangrove area. Turner (1977) found a positive correlation between penaeid shrimp catches and the vegetated surface area of estuaries in the Gulf of Mexico. Martosubroto and Naamin (1977), working in Indonesia, showed a positive correlation between annual fish landings and mangrove area. They implied that a certain minimum mangrove area is necessary for high production, a point also noted by Pauly and Ingles (1986) who suggested that the impact of destroying a mangrove area might be greater if the area is small and residual. A review of literature (Baran and Hambrey, 1998) demonstrated the dependence of fish harvests on estuarine environments, and showed the importance of these systems in terms of sustainable management of the coastal resource. Rönnbäck (1999) and Barbier (2000) identified and synthesised ecological and biophysical links of mangroves that sustain seafood production from an economic perspective, and Manson et al. (2005) tried to go beyond the correlative approach and developed a new framework on which evaluations can be based.

The review presented here found a total of 27 studies comparing commercial catch with estuarine habitats, in particular mangroves in tropical and subtropical zones, over the last four decades. Most of the analyses in these studies have resulted in positive correlations, assuming that the area of mangroves or tidal wetland habitat directly translates to the catch of commercial fisheries (Manson et al., 2005; Meynecke et al., 2007). Estimates of the amount of commercial catch explained by the presence of mangroves or estuaries range from 20 to 90% (Fig. 1). The most common variables used were mangrove area, followed by linear extent and intertidal area or estuarine size. Over 15 studies used mangroves as a proxy and seven studies used the extent of estuaries, coastal vegetation or shallow water. Most studies were undertaken in Australia, Asia and the U.S.A., whereas West Africa and South America were under-represented (see also Faunce and Serafy, 2006, in their review on mangroves–fish studies). Estimates in studies covering worldwide tropical commercial catch range between 21% (Houde and Rutherford, 1993) and 30% (Naylor et al., 2000) for an estuarine–fish catch relationship, 38% for a mangrove–prawn catch relationship (Lee, 2004), 53% for a mangrove area–fish catch relationship (Pauly and Ingles, 1986), and 54% for an intertidal wetlands–prawn catch relationship (Turner, 1977).

Depending on species, location and time scale, the relationships between commercial catch and mangroves vary largely, indicating that the link is more complex than a linear function. The predictors used in the regression analyses are themselves strongly correlated, and catch statistics are often not well delineated. There is high variation within the data sets (mangrove forest distribution, commercial records, effect of stock size and fishing pressure) and difficulty in distinguishing links against a background of highly variable temperature, rainfall, ocean currents, and fishing effort.

On the other hand, estuarine or lagoonal habitats and the strong links between them have been neglected in past studies (Sheridan and Hays, 2003). A certain combination of habitats and their accessibility is likely to explain the importance of estuaries to nekton (Cappo et al., 1998). Evidence is mounting that permanently inundated fringing mangroves in the Caribbean primarily serve as daytime refugia for a major component of fishes occupying various habitats in lagoons or bays (Nagelkerken et al., 2000a; Valdés-Muñoz and Mochek, 2001), while fishes from adjacent habitats feed in large intertidal mangroves at high tide (Sheaves, 2005; Lugendo et al., 2007b). This suggests for some species that fish production attributed to mangroves may not necessarily be derived from this habitat alone. Evidence exists, for example, that fish abundance and species richness are higher when mangroves and seagrass beds occur together rather than in isolation (Robertson and Blaber, 1992; Nagelkerken et al.,

Fig. 1. World map showing the percentage of commercial fish catch explained by either mangroves or estuarine presence from 27 reviewed studies of which 22 provided quantitative data for this linkage. For countries where more than one study was conducted the conservative number has been chosen for display (for a detailed listing see Manson et al., 2005; Meynecke et al., 2007).

2001; Dorenbosch et al., 2006a,b; Jelbart et al., 2007). Many fish species occupying lagoons appear to show ontogenetic fish movements between seagrass beds, tidal channels and mangroves (Rooker and Dennis, 1991; Nagelkerken et al., 2000c; Nagelkerken and van der Velde, 2002, 2003; Eggleston et al., 2004; Lugendo et al., 2005), making the individual contribution of mangroves difficult to determine (Adams et al., 2006).

Worldwide, most studies on mangrove fish communities and their linkages with offshore fisheries have been done in estuarine mangrove systems (Nagelkerken, 2007). However, there are hundreds to thousands of small islands in the Caribbean and Indo-Pacific which only harbour non-estuarine mangroves located in marine embayments and lagoons. Although their surface area is mostly much smaller than that of large estuarine mangrove forests, they may be important on an island scale for coral-reef associated fisheries. Only in this millennium have studies started focusing in more detail on the connectivity between non-estuarine mangroves (and seagrass beds) and adjacent coral reefs with regard to fish movement (Nagelkerken, 2007), mostly based on multiple habitat density comparisons using a single census technique and distinguishing between fish size classes. This has resulted in the identification of several (commercial) reef fish species which appear to depend on mangroves while juvenile (e.g., Nagelkerken et al., 2000b,c; Cocheret de la Morinière et al., 2002; Christensen et al., 2003; Serafy et al., 2003; Eggleston et al., 2004; Dorenbosch et al., 2007). Studies comparing reef fish communities near and far from mangrove habitats, and with the presence or absence of island mangroves, have shown that the dependence on mangroves is species-specific, but appears to be high for various reef species (Nagelkerken et al., 2000b, 2001, 2002; Mumby et al., 2004; Dorenbosch et al., 2004, 2005, 2006a,b, 2007). Otolith microchemistry studies have also suggested a linkage between mangroves and coral reefs (Chittaro et al., 2004). Mumby (2006) developed algorithms to describe various aspects of mangrove–reef connectivity that can be used for management purposes.

Future investigations of tidal wetlands–fisheries links, should be based on an understanding of connectivity and should use standardised data collection. More research is required documenting the natural temporal and spatial variability of assemblages in fish habitats. Although there is no direct evidence of the fish catch–mangrove dependence, studies so far clearly infer a strong link emphasising the need to reverse the loss of mangroves and tidal wetlands (FAO, 2003) from both natural and anthropogenic causes.

11. Mangroves as habitats for amphibians and reptiles

Several independent evolutionary lines of reptiles and amphibians have successfully colonised, and are variously dependent on, mangrove ecosystems. These include frogs, marine and freshwater turtles, crocodilians, lizards, and marine and terrestrial snakes.

11.1. Frogs

Globally, little is known of the amphibian fauna inhabiting mangroves (Kathiresan and Bingham, 2001). Amphibians are generally intolerant of saline conditions found within mangroves, although many species are associated with estuarine habitats such as frog species from the genus *Eleutherodactylus* (Hedges and Thomas, 1992). Notable exceptions include the crab-eating frog *Rana cancrivora* from Southeast Asia that is adapted to salt water during all stages of its life cycle (Dunson, 1977), and *E. caribe* which is unique among species in the genus by inhabiting the flooded, *Rhizophora mangle*-dominated mangrove habitat of the Tiburon Peninsula of Haiti in the Caribbean (Hedges and Thomas, 1992).

11.2. Turtles

Freshwater turtles are known to inhabit estuaries, but little is known of their specific habitat requirements. The mangrove terrapin *Batagur baska* (from Central and Southeast Asia), and the painted terrapin *Callagur borneoensis* (from the Sundarbans, Bangladesh) are large freshwater chelonians that are known to inhabit tidal creeks and rivers (Blanco et al., 1991). Both species are listed as critically endangered and rely on riparian vegetation, including mangrove fruit, as a food source (IUCN, 2006; UNEP-WCMC, 2007). *Callagur borneoensis* nests on ocean beaches and the hatchlings have to swim through seawater to reach the river mouths; however, they are not physiologically adapted to the high water salinity in estuaries for extended periods (Dunson and Moll, 1980).

Five species of marine turtles have global distributions in tropical and temperate waters ranging from the lower reaches of estuaries to oceanic/pelagic habitats, while two species have relatively restricted ranges: the flatback turtle *Natator depressus* is endemic to the Australian-New Guinea continental shelf (Limpus and Chatto, 2004), and the Kemp's ridley turtle *Lepidochelys kempii* is restricted to the warm temperate zone of the North Atlantic Ocean (Bowen et al., 1997). Marine turtles occupy different habitats at different stages of their life cycle: natal beaches, mating areas, inter-nesting habitat, feeding areas and pelagic waters (EA, 2003). Juvenile movements in neritic developmental habitats are little known compared to adult reproductive migrations. There is also a lack of knowledge of life history and habitat requirements away from nesting beaches. Habitat selection may be significantly influenced by biotic factors such as the availability and/or quality of food or the co-occurrence of predators. In nearshore waters, abiotic factors such as tidal flux, water temperature and depth, salinity and turbidity may influence the occurrence of marine turtles via direct (physiological tolerance) or indirect (effects on prey or predators) mechanisms (EA, 2003). Habitat quality for *L. kempii* in the nearshore waters of the north-western Gulf of Mexico was influenced by water temperature and depth, salinity, dissolved oxygen and turbidity, which influenced the distribution and abundance of predators and prey (Metz, 2004). In general, there is a lack of detailed studies of the habitat requirements of in-water life history stages of marine turtles (Metz, 2004).

Many animals alter their movements and home range in relation to the particular type and quality of the habitat occupied. Fidelity of marine turtles to foraging areas has been demonstrated in several studies (Limpus and Limpus, 2000; Godley et al., 2002). Green turtles (*Chelonia mydas*) have a pelagic existence for the first 3–5 years, after which they recruit to coastal waters and occupy a series of developmental habitats, including mangroves, until sexual maturity (Makowski et al., 2005). These movements coincide with an ontogenetic dietary shift from an omnivorous to a herbivorous diet including *Avicennia marina* fruit (Pendoley and Fitzpatrick, 1999), cotyledons and propagules (Limpus and Limpus, 2000; H.M. Penrose, unpublished data). Indirectly, mangroves can provide a food source for marine turtles by providing habitat for macroalgae that grow on roots, trunks (Cribb, 1996) and pneumatophores (H.M. Penrose, unpublished data). *Rhizophora mangle* is also known as a developmental foraging ground for Kemp's ridley turtles in the coastal waters of their range (Schmid, 2000). Despite a paucity of data, evidence suggests that mangroves are important to marine turtles and further research is needed to determine species-specific differences in mangrove use in a range of environmental settings.

11.3. Crocodilians

The 23 extant crocodilian species (crocodiles, alligators, caimans and gharials) are integral components of aquatic, wetland and marine/estuarine ecosystems in tropical and subtropical regions, with most species requiring large areas of undisturbed habitat to maintain viable populations (Hutton and Webb, 1990). The relative importance of mangroves as a habitat for crocodilians, compared with other habitats, is variable, due to the wide diversity in their biology and ecology. However, as nurseries for fish and other marine animals on which crocodilians feed, mangroves provide an abundance of food sources at all life history stages. The estuarine crocodile *Crocodylus porosus* is one of the most notable species associated with mangroves. Generally, *C. porosus* do not nest in mangroves but are found nesting in vegetation fringing mangrove areas (Webb et al., 1977; Magnusson, 1980; Webb et al., 1983). However, the indirect importance of mangroves for *C. porosus* has been demonstrated in Sri Lanka where the decline of this species is linked to an increase in coastal runoff due to clearing of mangrove trees, resulting in the destruction of crocodile nests and eggs (Santiapillai and de Silva, 2001). Prop-roots of *Rhizophora* spp. are also known to provide an important structural refuge for hatchlings (Santiapillai and de Silva, 2001).

11.4. Lizards

Many lizard species, ranging from geckos to iguanas, are known to inhabit intertidal mangrove forests. Some lizards are terrestrial species that enter mangroves on an opportunistic basis to access resources, whereas others live a semi-aquatic existence, with the monitor lizards *Varanus* spp. being the most notable. The rusty monitor *Varanus semiremex*, which is restricted to the east coast of Queensland, Australia, are particularly dependent on *Avicennia marina*, utilising hollow limbs of living mature as well as dead trees (Wilson and Knowles, 1988).

11.5. Snakes

Pythons (*Python morolus*) and king cobras (*Ophiophagus hannah*) make opportunistic movements from terrestrial to intertidal mangrove habitats to feed (Macintosh and Ashton, 2002). Some sea snakes (family Hydrophiidae) access mangroves during high tide, whereas others, such as the 'primitive' *Ephalophis greyae* of Western Australia, which has retained its terrestrial mode of locomotion, undertake foraging migrations across the dry mangrove substrate during low tide in search of gobiid fish (Storr et al., 1986; H.M. Penrose, unpublished data). Other snake species rely on mangrove trees as a physical habitat structure, such as *Myron richardsonii* that is endemic to Northern Australia (Guinea et al., 2004), and *Boiga dendrophila* of Southeast Asia and Australia, both members of the family Colubridae (Macintosh and Ashton, 2002). The structure of snake communities in the mangroves of south-eastern Nigeria was described by Luiselli and Akani (2002). Eighteen snake species were recorded in mangroves, whereas 43 species inhabited neighbouring habitats (rainforest and forest-plantation mosaics). Of these 18 species, 50% were arboreal, 22% terrestrial, 11% terrestrial–arboreal, 11% semi-aquatic, and 6% described as very generalist. Species preyed on a wide range of organisms including lizards, birds, bird eggs, frogs, mammals and fish. The relative frequency of the African rock python *Python sebae* in the mangroves, compared with other habitats, suggest that mangroves may represent an important refuge or dispersal corridor for this threatened species. Luiselli and Akani (2002) highlight the need for further research on the rich diversity of the high trophic level arboreal snake species, and the preservation of the habitat mosaics within mangrove creeks, where the great majority of snakes are found.

12. Mangroves as habitats for birds

Mangrove habitats play host to a moderate number of bird species around the globe. Most diverse are the Queensland mangroves of Australia which host 186 bird species (Noske, 1996). Other counts are 135 in Peninsular Malaysia (Nisbet, 1968), 125 in Guinea-Bissau, West Africa (Altenburg and van Spanje, 1989), 104 in north-western Australia (Noske, 1996), 94 in Surinam (Haverschmidt, 1965), and 84 in Trinidad (Ffrench, 1966). The forests are strongly zoned with few tree species and a sparse understory producing a simple vertical profile.

When considering the bird faunas of these and other mangrove habitats around the globe, it is interesting to speculate on the sources of the species that make up these communities. To what extent have mangrove forests played the role of independent sites of species diversification, to what extent have they been recipient habitats, and to what extent have they been the source of colonists for other habitats? What ecological forces may have driven these processes? This suggests a way to review the avifauna of mangroves, namely those that have a tolerance for a narrow range of habitats (stenotopic species), mangrove invaders, and mangrove species that move out into other habitats.

12.1. Mangrove specialists

The first interesting observation is that there are few true mangrove specialists. No African species has been found to be exclusively mangrove-dependent, the closest being the insectivorous sunbird *Anthreptes gabonicus* which is found in mangroves but also in riverine woods hundreds kilometres inland. Mangrove habitats in Surinam host 94 bird species, while in Trinidad these habitats support 84 bird species. Only one species, the rufous crab–hawk (*Buteogallus aequinoctialis*) is restricted there to mangrove habitats (Haverschmidt, 1965; Ffrench, 1966). In north-western Australia, 16 of 104 species are more or less confined to mangroves, in eastern Australia, 9 of 106. Just 11 species are mangrove-dependent there, namely great-billed heron *Ardea sumatrana*, striated heron *Butorides striata*, chestnut rail *Eulabeornis castaneoventris*, collared kingfisher *Todiramphus chloris*, mangrove robin *Peneoenanthe pulverulenta*, kimberley flycatcher *Microeca flavigaster tormenti*, white-breasted whistler *Pachycephala lanioides*, dusky gerygone *Gerygone tenebrosa*, yellow silver-eye *Zosterops lutea*, red-headed myzomela *Myzomela erythrocephala*, and mangrove honeyeater *Lichenostomus fasciogularis*.

In Peninsular Malaysia, Wells (1999) cites nine species (brown-winged kingfisher *Pelargopsis amauroptera*, ruddy kingfisher *Halcyon coromanda*, greater goldenback *Chrysocolaptes lucidus*, mangrove pitta *Pitta megaryncha*, black-hooded oriole *Oriolus xanthornus*, great tit *Parus major*, dusky warbler *Phylloscopus fuscatus* (a non-breeding visitor), mangrove blue flycatcher *Cyornis rufigastra*, and copper-throated sunbird *Leptocoma calcostetha*) that depend exclusively on mangrove forests, or mangrove forest out to an immediate fringe of Nipa palm swamp or strand or plantation woodland. Three others (great-billed heron *Ardea sumatrana*, great egret *Ardea alba*, and milky stork *Mycteria cinerea*) depend on it exclusively for nesting but feed elsewhere. Grey heron *Ardea cinerea*, striated heron, and black-crowned night heron *Nycticorax nycticorax* now also breed inland. Only the brown-winged kingfisher, mangrove pitta, and copper-throated sunbird are global mangrove specialists. In regions outside the peninsula some of these specialists use other habitats. Ruddy kingfishers and great tits inhabit inland forests in Thailand, and the laced green woodpecker enters inland forest north of latitude 60°N. The fact that none of these birds has invaded inland non-forest habitats suggests that the peninsular populations have become specialised for mangrove habitats. The abundant, mainly frugiverous, families of adjacent dipterocarp evergreen forest are conspicuously rare, namely babblers, barbets, bulbuls, leafbirds, hornbills, and pheasants.

12.2. Mangrove invaders

In some cases, species may be better adapted to non-mangrove habitats but use mangrove either because their preferred habitats are not available locally, or because some mangrove forests provide marginal habitat for some individuals whose principal populations occupy other adjacent forest habitats. Wells (1999) analysed the species origins of the birds in mangroves of Peninsular Malaysia, where inland forests once abutted with mangrove trees over long stretches of the coast until well into the 20th century. Around one-third of the avian mangrove community (mainly kingfishers, sunbirds, warblers and woodpeckers) is shared with its former inland forest habitats which may indicate how marginal mangroves were for at least some of the inland forest species that used their back zone. Leafbirds, broadbills, giant woodpeckers, and others formerly reported in the mangroves are now scarce or absent. Wells (1999) suggested that if more of the interface between mangroves and inland forests had been explored before the interface had been destroyed, more shared species may have been found in the mangroves. The same may be true in Western Australia, where the proximity of mangroves and so-called vine forests may maintain species in mangroves (Noske, 1996).

Given the nature of some current mangrove specialists, it seems likely that mangroves were attractive for some open-forest adapted species. The latter habitats would have been much drier during the Pleistocene glacial periods, while the mangroves were probably more extensive providing an essential refuge for birds from shrinking open forests. Noske (1996) cites the existence of mangrove specialists such as mangrove fantail *Rhipdura phasiana*, broad-billed flycatcher *Myiagra ruficollis*, kimberley flycatcher, mangrove gerygone *Gerygone levigaster*, and mangrove honeyeater, species with relatives in these open forest regions, and even inland regions. However, given the huge linear continuity of continental mangrove forests, it is almost impossible to guess where any particular specialist originated.

12.3. Species that move out to non-mangrove habitats

Some scientists suggest that the mangrove assemblage is an exporter of bird species to non-forest habitats. This assumption is based on the birds having niches that developed in an environment of low plant species diversity, itself derived from instability of the habitat over various time scales. This, in turn, results in a relatively simple structure and reduced niche space. Bird species niches are broad enough to predispose mangrove birds to simplicity and instability elsewhere (Noske, 1995; Ward, 1968). Noske (1995) revealed that certain groups (woodpeckers, passerines) found both in mangroves and non-forest habitats have narrower niches than those species that still live exclusively within the mangroves, perhaps because of competition once outside the mangrove habitat, or because the simplicity of the mangroves precluded such specialisation.

Ward (1968) remarked how mangroves have contributed many bird species to rural and urban habitats in Peninsular Malaysia, and suggested that this may be due to the simple floristic and habitat structure shared by mangroves and these anthropogenic habitats. Broad niches and tolerances by mangrove bird species may enable them to exploit these newer habitats. Noske (1995) related broad niches of mangrove bird species to fluctuations in food availability driven by tidal cycles. He interpreted the absence of colonisation of Australian urban and exurban habitats by mangrove bird species as being a consequence of the sharp contrast between the stable, evergreen, fire-protected mangroves, and the highly seasonal, deciduous, and fire-prone savannas that abut them. An alternative explanation could be that such savannas never were empty of species as the suddenly deforested sub-coastal lowlands of Peninsular Malaysia, which provided the opportunity for colonisation (D.R. Wells, personal communication).

As a rule, most bird species found in mangroves are also found in other habitats, but how would we tell in which direction colonisation took place: into or out of mangroves? We know that most of the West African mangrove bird species in Guinea-Bissau were more common in adjoining forests and rice fields. Some use the mangrove for roosting only (Altenburg and van Spanje, 1989), and in Peninsular Malaysia 46 residents and at least 6 non-breeding visitors to mangroves also occur in 1 or more of the original inland forest formations (Wells, 1999). Some kinds of birds, such as aerial insectivores (nightjars, tree swifts, rollers, swallows), may nest in mangroves but feed over a wider range of habitats while others (white-vented myna *Acridotheres javanicus*, java sparrow *Lonchura oryzivora*) may nest in mangroves but never feed there (Medway and Wells, 1976).

Almost as many bird species that we now find in mangroves can also be found in open coastal areas, agricultural, and urban areas that meet the truncated mangrove succession inland. In Australia, the floristically rich north-eastern mangroves have fewer mangrove specialist bird species than the north-western mangroves, though it is unclear why. Mangrove habitats may have remained widespread during the Pleistocene glacial periods when rainforests may have contracted to small patches, providing places for many of the rainforest species to survive, and then have been a source for re-populating re-expanding rain forests.

12.4. Synthesis

The most intriguing insights of the role of mangroves for bird communities come from a consideration of mangroves in their broader context, namely their relationships with other habitats, both current and historic. We should also ask why there are so few true mangrove specialists. It is interesting to speculate on what current species may tell us about past habitat relationships. What roles may mangroves have served as stable habitats during times of climatic change in the past? We do not have an accepted model of how mangrove forest might have behaved in response to sea-level changes. While one can envisage the mangrove system extending seaward as sea levels fall, observation shows that a simple change in local long-shore currents can eliminate the forest, while a rising sea level would probably reduce mangroves. So what was the distribution and availability of mangroves in the past? How did changes in mangrove availability push species out into non-mangrove habitats? We can imagine a scenario where mangroves change sequentially from becoming refugia for drying forests to expellers of birds as they shrink with rising sea levels, and a resulting two-way flow of species into and out of these habitats over time.

It is not clear to what extent mangrove forests support relict populations. Noske (1995) reports that one of his transects in Malaysia still retained small areas of original back-mangrove forest, and several decades after the link with inland forest was broken this still contained a few ‘inland forest’ birds, such as velvet-fronted nuthatch *Sitta frontalis*. Bird species of adjacent inland habitats, and those habitats formerly adjacent before their destruction, use mangroves in different ways.

As one would predict, the greatest bird species diversity occurred in the more plant-species diverse back-mangrove zones, where colonisation of the mangrove from the inland species once occurred, and where it interfaces with habitats inland (Wells, 1999). Nisbet (1968) suggested that the current scarcity of overlapping forest bird species in the mangroves of Peninsular Malaysia is the result of the near-total clearance of the transition zone between mangrove and inland forests. Some formerly widespread species of this zone, such as the giant woodpeckers, have all but disappeared from their mangrove haunts. Noske (1996) suggested that the relatively small number of mangrove bird specialists in Peninsular Malaysia resulted from long historical and continuous contact between mangrove and other forest habitats and so no geographical block to gene flow was present. However, Peninsular Malaysia has more species than West Africa and Surinam. This could in turn be explained by the direct contact of its mangrove ecosystem with that of the rest of tropical Asia, acting as a corridor for immigrants from outside rather than by generation of species from within the habitat.

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References

Abele, L.G., 1992. A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus. Smithson. Contr. Zool. 527.

Acosta, A., 1997. Use of multi-mesh gillnets and trammel nets to estimate fish species composition in coral reef and mangroves in the southwest coast of Puerto Rico. Caribb. J. Sci. 33, 45–57.

Adams, A.J., Dahlgren, C.P., Kellison, G.T., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I., Serafy, J.E., 2006. Nursery function of tropical back-reef systems. Mar. Ecol. Prog. Ser. 318, 287–301.

Ahmad Adnan, N., Loneragan, N.R., Connolly, R.M., 2002. Variability of, and the influence of environmental factors on, the recruitment of postlarval and juvenile *Penaeus merguiensis* in the Matang mangroves of Malaysia. Mar. Biol. 141, 241–251.

Aikanathan, S., Sasekumar, A., 1994. The community structure of macroalgae in a low shore mangrove forest in Selangor, Malaysia. Hydrobiologia 285, 131–137.

Alcolado, P.M., 1991. General features of Cuban sponge communities. In: Rützler, K. (Ed.), New Perspectives in Sponge Biology. Smithsonian Inst. Press, Washington, DC, pp. 351–357.

Alongi, D.M., 1987a. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. Mar. Ecol. Prog. Ser. 40, 103–114.

Alongi, D.M., 1987b. Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. Mar. Biol. 95, 447–458.

Alongi, D.M., 1987c. The influence of mangrove-derived tannins on intertidal meiobenthos in tropical estuaries. Oecologia 71, 537–540.

Alongi, D.M., 1990. Community dynamics of free-living nematodes in some tropical mangrove and sandflat habitats. Bull. Mar. Sci. 46, 358–373.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Alongi, D.M., Christoffersen, P., 1992. Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. Mar. Ecol. Prog. Ser. 81, 229–245.

Altenburg, W., van Spanje, T., 1989. Utilization of mangroves by birds in Guinea-Bissau. Ardea 77, 57–74.

Alvarez-Leon, R. 1983. Mangrove ecosystems of Colombia. Conservation and sustainable utilization of mangrove forests in Latin America and Africa Regions. ITTO/ISME Project PD114/90, Yokohama, Japan, pp. 75–113.

Angelici, F.M., Politano, E., Bogudue, A.J., Luiselli, L., 2005. Distribution and habitat of otters (*Aonyx capensis* and *Lutra maculicollis*) in southern Nigeria. Ital. J Zool. 72, 223–227.

Ansari, Z.A., Sreepada, R.A., Matondkar, S.G.P., Parulekar, A.H., 1993. Meiofaunal stratification in relation to microbial food in a tropical mangrove mud flat. Trop. Ecol. 34, 204–216.

Ashton, E.C., 1999. Biodiversity and community ecology of mangrove plants, molluscs and crustaceans in two mangrove forests in Peninsular Malaysia in relation to management practices. Ph.D. Thesis. University of York, UK.

Ashton, E.C., 2002. Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. J. Exp. Mar. Biol. Ecol. 273, 97–119.

Ballantyne, L.A., 1987. Further revisional studies on the firefly genus *Pteroptyx* Olivier (Coleoptera: Lampyridae: Luciolinae: Luciolini). Trans. Am. Entomol. Soc. 113, 117–169.

Ballantyne, L.A., McLean, M.R., 1970. Revisional studies on the firefly genus *Pterotyx* Olivier (Coleoptera: Lampyridae: Luciolinae: Luciolini). Trans. Am. Entomol. Soc. 96, 223–305.

Baran, E., 1999. A review of quantified relationships between mangroves and coastal resources. Res. Bull. Phuket Mar. Biol. Cent. 62, 57–64.

Baran, E., Hambrey, J., 1998. Mangrove conservation and coastal management in southeast Asia: What impact on fishery resources? Mar. Poll. Bull. 37, 431–440.

Baran, E., Albaret, J.J., Diouf, P.S., 1999. Les écosystèmes à mangroves: les mangroves des rivières du Sud—les peuplements de poissons: places des communautes de poissons dans les écosystèmes à mangrove. In: Cormier-Salem, M.C. (Ed.), Rivières du Sud. Societés et mangroves ouest-africaines (du Sénègal à la Sierra Leone), vol. 1. IRD Editions, Paris, pp. 98–116.

Barbier, E.B., 2000. Valuing the environment as input: review of applications to mangrove-fishery linkages. Ecol. Econ. 35, 47–61.

Barbier, E.B., Strand, I., 1998. Valuing mangrove-fishery linkages—a case study of Campeche, Mexico. Environ. Resour. Econ. 12, 151–166.

Barletta, M., Barletta-Bergen, A., Saint-Paul, U., Hubold, G., 2005. The role of salinity in structuring the fish assemblages in a tropical estuary. J. Fish Biol. 66, 45–72.

Barnes, D.K.A., 1999. High diversity of tropical intertidal zone sponges in temperature, salinity and current extremes. Afr. J. Ecol. 37, 424–434.

Barnes, D.K.A., Bell, J.J., 2002. Coastal sponge communities of the West Indian Ocean: taxonomic affinities, richness and diversity. Afr. J. Ecol. 40, 337–349.

Barrett, M.A., Stiling, P., 2006. Effects of key deer herbivory on forest communities in the lower Florida Keys. Biol. Conserv. 129, 100–108.

Bartsch, I., 2003. Mangrove halacarid fauna (Halacaridae, Acari) of the Dampier region, Western Australia, with description of five new species. J. Nat. Hist. 37, 1855–1877.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51, 633–641.

Benfield, M.C., Bosschieter, J.R., Forbes, A.T., 1990. Growth and emigration of *Penaeus indicus* H. Milne-Edwards (Crustacea: Decapoda: Penaeidae) in the St. Lucia Estuary, southern Africa. Fish. Bull. U.S. 88, 21–28.

Bingham, B.L., Young, C.M., 1991. Influence of sponges on invertebrate recruitment: a field test of allelopathy. Mar. Biol. 109, 19–26.

Bingham, B.L., Young, C.M., 1995. Stochastic events and dynamics of a mangrove root epifaunal community. PSZNI: Mar. Ecol. 16, 145–163.

Blaber, S.J.M., 1980. Fishes of the Trinity Inlet system of North Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Aus. J. Mar. Freshwater Res. 31, 137–146.

Blaber, S.J.M., 1987. Factors affecting recruitment and survival of Mugilidae in estuaries and coastal waters of the Indo-West Pacific. Am. Fish. Soc. Symp. 1, 507–518.

Blaber, S.J.M., 2000. Tropical Estuarine Fishes: Ecology, Exploitation and Conservation. Blackwell, Oxford.

Blaber, S.J.M., 2007. Mangroves and fishes: issues of diversity, dependence, and dogma. Bull. Mar. Sci. 80, 457–472.

Blaber, S.J.M., Blaber, T.G., 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish Biol. 17, 143–162.

Blaber, S.J.M., Cyrus, D.P., 1981. A revised checklist and further notes on the fishes of the Kosi system. Lammergeyer 31, 5–14.

Blaber, S.J.M., Milton, D.A., 1990. Species composition, community structure and zoogeography of fishes of mangroves in the Solomon Islands. Mar. Biol. 105, 259–268.

Blaber, S.J.M., Young, J.W., Dunning, M.C., 1985. Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of north-west Australia. Aus. J. Mar. Freshwater Res. 36, 247–266.

Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1989. Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Est. Coast. Shelf Sci. 29, 509–531.

Blanco, S., Behler, J.L., Kostel, F., 1991. Propogation of the Batagurine Turtles *Batagur baska* and *Callagur borneoensis* at the Bronx Zoo. In: Beaman, K.R., Caporaso, F., McKeown, S., Graff, M.D. (Eds.), Proceedings of the 1st International Symposium on Turtles and Tortoises: Conservation and Captive Husbandry. pp. 63–65.

Bordignon, M.O., 2006. Diet of the fishing bat *Noctilio leporinus* (Linnaeus) (Mammalia, Chiroptera) in a mangrove area of southern Brazil. Rev. Bras. Zool. 23, 256–260.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay. Biodivers. Conserv. 13, 1059–1074.

Bosire, J.O., Kairo, J.G., Kazungu, J., Koedam, N., Dahdouh-Guebas, F., 2005. Predation on propagules regulates regeneration in a high-density reforested mangrove plantation. Mar. Ecol. Prog. Ser. 299, 149–155.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Boto, K.G., Robertson, A.I., 1990. The relationship between nitrogen fixation and tidal exports of nitrogen in a tropical mangrove system. Est. Coast. Shelf Sci. 31, 531–540.

Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130, 441–448.

Bouillon, S., Moens, T., Overmeer, I., Koedam, N., Dehairs, F., 2004. Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. Mar. Ecol. Prog. Ser. 278, 77–88.

Bouillon, S., Connolly, R., Lee, S.Y., 2008. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res., doi:10.1016/j.seares.2007.05.001, in press.

Bowen, B.W., Clark, A.M., Abreu-Grobois, F.A., Chaves, A., Reichart, H.A., Ferl, R.J., 1997. Global phylogeography of the ridley sea turtle (*Lepidochelys* spp.) as inferred from Mitochondrial DNA sequences. Genetica 101, 179–189.

Branch, G.M., Branch, M.L., 1980. Competition in *Bembicium auratum* (Gastropoda) and its effect on microalgal standing stocks in mangrove muds. Oecologia 46, 106–114.

Buck, J., Buck, E., 1976. Synchronous fireflies. Sci. Am. 234 74–79, 82–85.

Burrows, D.W., 2003. The role of insect leaf herbivory on the mangroves *Avicennia marina* and *Rhizophora stylosa*. Ph.D. Thesis. James Cook University, Australia.

Camilleri, J.C., 1992. Leaf-litter processing by invertebrates in a mangrove forest in Queensland. Mar. Biol. 114, 139–145.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Cantera, J., Arnaud, P.M., Thomassin, B.A., 1983. Biogeographic and ecological remarks on molluscan distribution in mangrove biotopes. 1. Gastropods. J. Molluscan Stud. 49, 10–26.

Cappo, M., Alongi, D.M., Williams, D.Mc.B., Duke, N.C., 1998. A Review and Synthesis of Australian Fisheries habitat research. Major Threats, Issues and Gaps in Knowledge of Marine and Coastal Fisheries Habitats—A Prospectus of Opportunities for the FRDC "Ecosystem protection program" Australian Institute of Marine Science, Townsville, Australia.

Carballo, J.L., 2000. Distribution of *Ecteinascidia turbinata* (Ascidiacea: Perophoridae) in mangroves of the Yucatan Peninsula, Mexico. Rev. Biol. Trop. 48, 365–369.

Carlén, A., Ólafsson, E., 2002. The effects of the gastropod *Terebralia palustris* on infaunal communities in a tropical tidal mud-flat in East Africa. Wetl. Ecol. Manage. 10, 303–311.

Chittaro, P.M., Fryer, B.J., Sale, P.F., 2004. Discrimination of French grunts (*Haemulon flavolineatum*, Desmarest, 1823) from mangrove and coral reef habitats using otolith microchemistry. J. Exp. Mar. Biol. Ecol. 308, 169–183.

Chong, V.C., 1995.In: The Prawn–Mangrove Connection—Fact or Fallacy? Paper presented at the JIRCA Seminar: "Productivity and Sustainable Utilization of Brackish Water Mangrove Ecosystem". 12–13 December, 1995, Hotel Equatorial International, Kuala Lumpur, Malaysia.

Chong, V.C., Sasekumar, A., 1981. Food and feeding habits of the white prawn *Penaeus merguiensis*. Mar. Ecol. Prog. Ser. 5, 185–191.

Chong, V.C., Sasekumar, A., Leh, M.U.C., D'Cruz, R., 1990. The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. Est. Coast. Shelf Sci. 31, 703–722.

Chong, V.C., Sasekumar, A., Wolanski, E., 1996. The role of mangroves in retaining penaeid prawn larvae in Klang Strait, Malaysia. Mangroves Salt Marshes 1, 11–22.

Chong, V.C., Low, C.B., Ichikawa, T., 2001. Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. Mar. Biol. 138, 77–86.

Christensen, J.T., Sauriau, P.G., Richard, P., Jensen, P.D., 2001. Diet in mangrove snails: preliminary data on gut contents and stable isotope analysis. J. Shellfish Res. 20, 423–426.

Christensen, J.D., Jeffrey, C.F.G., Caldow, C., Monaco, M.E., Kendall, M.S., Appeldoorn, R.S., 2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf Caribb. Res. 14, 9–27.

Christensen, V., Pauly, D., 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61, 169–185.

Clayton, D.A., 1993. Mudskippers. Mar. Biol. Oceanogr. Annu. Rev. 31, 507–577.

Cocheret de la Morinière, E., Pollux, B.J.A., Nagelkerken, I., van der Velde, G., 2002. Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Est. Coast. Shelf Sci. 55, 309–321.

Cocheret de la Morinière, E., Nagelkerken, I., van der Meij, H., van der Velde, G., 2004. What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? Mar. Biol. 144, 139–145.

Coles, R.G., Lee Long, W.J., 1985. Juvenile prawn biology and the distribution of seagrass prawn nursery grounds in the southeastern Gulf of Carpentaria. In: Second Australian National Prawn Seminar. pp. 55–60.

Collins, M.S., 1969. Water relations in termites. In: Krishna, K., Weesner, F.M. (Eds.), Biology of Termites, vol. 1. Academic Press, New York/London, pp. 433–458.

Connolly, R.M., 1999. Saltmarsh as habitat for fish and nektonic crustaceans: challenges in sampling designs and methods. Aust. Ecol. 24, 422–430.

Corbet, A.S., Pendlebury, H.M., 1992. The Butterflies of the Malay Peninsula, fourth ed. Revised by Eliot, J.N. Malayan Nature Society, Kuala Lumpur.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Coull, B.C., 1999. Role of meiofauna in estuarine soft-bottom habitats. Aust. J. Ecol. 24, 327–343.

Coull, B.C., Greenwood, J.G., Fielder, D.R., Coull, B.A., 1995. Subtropical Australian juvenile fish eat meiofauna: experiments with winter whiting *Sillago maculata* and observations on other species. Mar. Ecol. Prog. Ser. 125, 13–19.

Cribb, A.B., 1996. Seaweeds of Queensland: A Naturalist's Guide. The Queensland Naturalists' Club Inc., Brisbane, Queensland.

Crona, B.I., Rönnbäck, P., 2005. Use of replanted mangroves as nursery grounds by shrimp communities in Gazi Bay, Kenya. Est. Coast. Shelf Sci. 65, 535–544.

Cuaron, A.D., Martinez-Morales, M.A., McFadden, K.W., Valenzuela, D., Gompper, M.E., 2004. The status of dwarf carnivores on Cozumel Island, Mexico. Biodivers. Conserv. 13, 317–331.

Cyrus, D.P., Blaber, S.J.M., 1987a. The influence of turbidity on juvenile marine fishes in estuaries. Part 1, field studies. J. Exp. Mar. Biol. Ecol. 109, 53–70.

Cyrus, D.P., Blaber, S.J.M., 1987b. The influence of turbidity on juvenile marine fishes in estuaries. Part 2, laboratory studies. J. Exp. Mar. Biol. Ecol. 109, 71–91.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Koedam, N., 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347, 83–89.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Van Speybroeck, D., Koedam, N., 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshwater Res. 49, 345–350.

Dahdouh-Guebas, F., Giuggioli, M., Oluoch, A., Vannini, M., Cannicci, S., 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bull. Mar. Sci. 64, 291–297.

Dahdouh-Guebas, F., Kairo, J.G., Jayatissa, L.P., Cannicci, S., Koedam, N., 2002. An ordination study to view vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka. Plant Ecol. 161, 123–135.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Vrancken, D., Ravishankar, T., Koedam, N., 2006. Short-term mangrove browsing by feral water buffalo: conflict between natural resources, wildlife and subsistence interests? Environ. Conserv. 33, 157–163.

Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Layman, C.A., Ley, J.A., Nagelkerken, I., Serafy, J.E., 2006. Marine nurseries and effective juvenile habitats: concepts and applications. Mar. Ecol. Prog. Ser. 312, 291–295.

Dall, W., 1981. Osmotic regulation of penaeid prawns in inshore and estuarine environments. Bull. Mar. Sci. 31, 812.

Dall, W., Hill, B.J., Rothlisberg, P.C., Staples, D.J., 1990. The biology of the Penaeidae. Adv. Mar. Biol. 27.

Daniel, P.A., Robertson, A.I., 1990. Epibenthos of mangrove waterways and open embayments: community structure and the relationship between exported mangrove detritus and epifaunal standing stocks. Est. Coast. Shelf Sci. 31, 599–619.

Davis, T.L.O., 1985. The food of barramundi, *Lates calcarifer* (Bloch), in coastal and inland waters of Van Diemen Gulf and the Gulf of Carpentaria, Australia. J. Fish Biol. 26, 669–682.

Decraemer, W., Coomans, A., 1978. Scientific report on the Belgian expedition to the Great Barrier Reef in 1967. Nematodes 13. A description of four new species and a redescription of four known species from in and around mangroves on Lizard Island. Aust. J. Mar. Freshwater Res. 29, 509–541.

Diaz, M.C., Smith, K.P., Rützler, K., 2004. Sponge species richness and abundance as indicators of mangrove epibenthic community health. Atoll Res. Bull. 518, 1–17.

Dittel, A.I., Epifanio, C.E., Cifuentes, L.A., Kirchman, D.L., 1997. Carbon and nitrogen sources for shrimp postlarvae fed natural diets from a tropical mangrove system. Est. Coast. Shelf Sci. 45, 629–637.

Dor, I., Levy, I., 1984. Primary productivity of the benthic algae in the hard bottom mangal of Sinai. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal—The Ecosystem of the Mangrove Forest. Developments in Hydrobiology 20. Dr. W. Junk Publishers, The Hague, pp. 179–191.

Dorenbosch, M., van Riel, M.C., Nagelkerken, I., van der Velde, G., 2004. The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. Est. Coast. Shelf Sci. 60, 37–48.

Dorenbosch, M., Grol, M.G.G., Christianen, M.J.A., Nagelkerken, I., van der Velde, G., 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. Mar. Ecol. Prog. Ser. 302, 63–76.

Dorenbosch, M., Grol, M.G.G., Nagelkerken, I., van der Velde, G., 2006a. Different surrounding landscapes may result in different fish assemblages in East African seagrass beds. Hydrobiologia 563, 45–60.

Dorenbosch, M., Grol, M.G.G., Nagelkerken, I., van der Velde, G., 2006b. Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. Biol. Conserv. 129, 277–282.

Dorenbosch, M., Verberk, W.C.E.P., Nagelkerken, I., van der Velde, G., 2007. Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Mar. Ecol. Prog. Ser. 334, 103–116.

Duke, N.C., 1992. Mangrove floristics and biogeography. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC. Coast. Est. Stud. 41, 63–100.

Dunlap, M., Pawlik, J.R., 1996. Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. Mar. Biol. 126, 117–123.

Dunlap, M., Pawlik, J.R., 1998. Spongivory by parrotfish in Florida mangrove and reef habitats. PSZNI: Mar. Ecol. 19, 325–337.

Dunson, W.A., 1977. Tolerance of high temperature and salinity by tadpoles of the Philippine frog, *Rana cancrivora*. Copeia 1977, 375–378.

Dunson, W.A., Moll, E.O., 1980. Osmoregulation in sea water of hatchling emydid turtles, *Callagur borneoensis*, from a Malaysian sea beach. J. Herpetol. 14, 31–36.

EA, 2003. Recovery Plan for Marine Turtles in Australia. Marine Species Section Approvals and Wildlife Division. Environment Australia, Canberra.

Eggleston, D.B., Dahlgren, C.P., Johnson, E.G., 2004. Fish density, diversity, and size-structure within multiple back reef habitats of Key West national wildlife refuge. Bull. Mar. Sci. 75, 175–204.

Ellison, A.M., Farnsworth, E.J., Merkt, R.E., 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. Glob. Ecol. Biogeogr. 8, 95–115.

Ellison, A.M., Farnsworth, E.J., 1990. The ecology of Belizean mangrove-root fouling communities: I. epibenthic fauna are barriers to isopod attack of red mangrove roots. J. Exp. Mar. Biol. Ecol. 142, 91–104.

Ellison, A.M., Farnsworth, E.J., 1992. The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. Hydrobiologia 247, 87–98.

Ellison, A.M., Farnsworth, E.J., Twilley, R.R., 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77, 2431–2444.

Emmerson, W.D., McGwynne, L.E., 1992. Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* de Man in relation to leaf litter production in Mgazana, a warm-temperate southern African mangrove swamp. J. Exp. Mar. Biol. Ecol. 157, 41–53.

Engel, S., Pawlik, J.R., 2000. Allelopathic activities of sponge extracts. Mar. Ecol. Prog. Ser. 207, 273–281.

Engel, S., Pawlik, J.R., 2005. Interactions among Florida sponges. II. Mangrove habitats. Mar. Ecol. Prog. Ser. 303, 145–152.

FAO, 2003. Status and trends in mangrove area extent worldwide. In: Wilkie, M.L., Fortuna, S. (Eds.), Forest Resources Assessment Working Paper No. 63. Forest Resources Division, FAO, Rome.

FAO, 2004. The State of World Fisheries and Aquaculture (SOFIA). FAO, Rome.

Farnsworth, E.J., Ellison, A.M., 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecol. Monogr. 66, 45–66.

Faunce, C.H., Serafy, J.E., 2006. Mangroves as fish habitat: 50 years of field studies. Mar. Ecol. Prog. Ser. 318, 1–18.

Fell, J.W., Cefalu, R.C., Masters, I.M., Tallman, A.S., 1975. Microbial activity in the mangrove (*Rhizophora mangle*) leaf detritus system. In: Walsh, G.E., Snedakar, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on the Biology and Management of Mangroves, Honolulu, 1974, University of Florida, Gainsville, pp. 661–679.

Feller, I.C., 2002. The role of herbivory by wood-boring insects in mangrove ecosystems in Belize. Oikos 97, 167–176.

Feller, I.C., Mathis, W.N., 1997. Primary herbivory by wood-boring insects along an architectural gradient of *Rhizophora mangle*. Biotropica 29, 440–451.

Fernandes, M.E.B., Andrade, F.A.G., Silva, J.D.E., 2006. Diet of *Micoreus demerarae* (Thomas) (Mammalia, Didelphidae) associated with contiguous forests of mangrove and terra firme in Braganca, Para, Brazil. Rev. Bras. Zool. 23, 1087–1092.

Ferrari, F.D., Fornshell, J.A., Ong, L., Ambler, J.W., 2003. Diel distribution of copepods across a channel of an overwash mangrove island. Hydrobiologia 499, 147–159.

Ffrench, R.P., 1966. The utilization of mangroves by birds in Trinidad. Ibis 108, 423–424.

Ford, P., Tillman, P., Robson, B., Webster, I., 2005. Organic carbon deliveries and their flow related dynamics in the Fitzroy estuary. Mar. Poll. Bull. 51, 119–127.

Forys, E.A., Humphrey, S.R., 1996. Home range and movements of the lower keys marsh rabbit in a highly fragmented habitat. J. Mammal. 77, 1042–1048.

France, R., 1998. Estimation the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. J. Trop. Ecol. 14, 413–425.

Fratini, S., Cannicci, S., Vannini, M., 2001. Feeding clusters and olfaction in the mangrove snail *Terebralia palustris* (Linnaeus) (Potamididae: Gastropoda). J. Exp. Mar. Biol. Ecol. 261, 173–183.

Frith, D.W., Tantanasiriwong, R., Bhatia, O., 1979. Zonation and abundance of macrofauna on a mangrove shore, Phuket Island. Phuket Mar. Biol. Centre Res. Bull. 10, 1–37.

Frusher, S.D., Giddins, R.L., Smith, T.J., 1994. Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary: effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. Estuaries 17, 647–654.

Fry, B., Ewel, K.C., 2003. Using stable isotopes in mangrove fisheries research a review and outlook. Isot. Environ. Health Stud. 39, 191–196.

Garcia, S., Le Reste, L., 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Techn. Paper No. 203, pp. 1–215.

Gee, J.M., Somerfield, P.J., 1997. Do mangrove diversity and leaf litter decay promote meiofaunal diversity? J. Exp. Mar. Biol. Ecol. 218, 13–33.

Gerlach, S.A., 1958. Die mangroveregion tropischer küsten als lebensraum. Z. Morphol. Ökol. Tiere 46, 636–730.

Giddens, R.L., Lucas, J.S., Neilson, M.J., Richards, G.N., 1986. Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae). Mar. Ecol. Prog. Ser. 33, 147–155.

Gillikin, D.P., Kamanu, C.P., 2005. Burrowing in the East African mangrove crab, *Chiromantes ortmanni* (Crosnier, 1965) (Decapoda, Bracayura, Sesarmidae). Crustaceana 78, 1273–1275.

Glaser, M., 2003. Interrelations between mangrove ecosystems, local economy ad social sustainability in Caeté Estuary, North Brazil. Wetl. Ecol. Manage. 11, 265–272.

Godley, B.J., Richardson, S., Broderick, A.C., Coyne, M.S., Glen, F., Hays, G.C., 2002. Long-term satellite telemetry of the movements and habitat utilization by green turtles in the Mediterranean. Ecography 25, 352–362.

Gonzalez-Pena, Md.C., Anderson, A.J., Smith, D.M., Moreira, G.S., 2002. Effect of dietary cellulose on digestion in the prawn *Macrobrachium rosenbergii*. Aquaculture 211, 291–303.

Goodbody, I., 1961. Mass mortality of a marine fauna following tropical rains. Ecology 42, 150–155.

Goodbody, I., 2003. The ascidian fauna of Port Royal, Jamaica—I. Harbor and mangrove dwelling species. Bull. Mar. Sci. 73, 457–476.

Gopal, B., Chauhan, M., 2006. Biodiversity and its conservation in the Sundarban Mangrove Ecosystem. Aquat. Sci. 68, 338–354.

Grasso, M., 1998. Ecological-economic model for optimal mangrove trade off between forestry and fishery production: comparing a dynamic optimization and a simulation model. Ecol. Model. 112, 131–150.

Guinea, M.L., Limpus, C.J., Whiting, S.D., 2004.In: Marine snakes. In: National Oceans Office, Description of Key Species Groups in the Northern Planning Area. National Oceans Office, Hobart, Australia.

Gwyther, J., 2003. Nematode assemblages from *Avicennia marina* leaf litter in a temperate mangrove forest in south-eastern Australia. Mar. Biol. 142, 289–297.

Hanson, F.E., 1978. Comparative studies of firefly pacemakers. Federat. Proc. 37, 2158–2164.

Haverschmidt, F., 1965. The utilization of mangroves by South American birds. Ibis 107, 540–542.

Haywood, M.D.E., Staples, D.J., 1993. Field estimates of growth and mortality of juvenile banana prawns (*Penaeus merguiensis*). Mar. Biol. 116, 407–416.

Hedges, S.B., Thomas, R., 1992. A new marsh-dwelling species of *Eleutherodactylus* from Haiti (Anura: Leptodactylidae). J. Herpetol. 26, 191–195.

Hodda, M., Nicholas, W.L., 1986. Temporal changes in littoral meiofauna from the Hunter River Estuary. Aust. J. Mar. Freshwater Res. 37, 729–741.

Hogarth, P.J., 1999. The Biology of Mangroves. Oxford University Press, New York.

Hopper, B.E., Fell, J.W., Cefalu, R.C., 1973. Effect of temperature on life cycles of nematodes associated with the mangrove (*Rhizophora mangle*) detritus system. Mar. Biol. 23, 293–296.

Houde, E.D., Rutherford, E.S., 1993. Recent trends in estuarine fisheries: predictions of fish production and yield. Estuaries 16, 161–176.

Hughes, D.A., 1969. Responses to salinity change as a tidal transport mechanism of pink shrimp, *Penaeus duorarum*. Biol. Bull. 136, 44–53.

Hutton, J.M., Webb, G.J.M., 1990. An introduction to the farming of crocodilians. Workshop IUCN/SSC. Crocodile Specialist Group, Gainesville, FA.

Intachat, J., Holloway, J.D., Speight, M.R., 2005. A preliminary assessment of the diversity of geometroid moths within different types of forests in Peninsular Malaysia. Malay. Nat. J. 57, 1–28.

IUCN, 2006. 2006 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland. http://www.iucnredlist.org.

Jelbart, J.E., Ross, P.M., Connolly, R.M., 2007. Fish assemblages in seagrass beds are influenced by proximity of mangrove forests. Mar. Biol. 150, 993–1002.

Jiang, J.X., Li, R.G., 1995. An ecological study of the Mollusca in mangrove areas in the estuary of the Jiulong River. Hydrobiologia 295, 213–220.

Jones, D.A., 1984. Crabs of the mangal ecosystem. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal—The Ecosystem of the Mangrove Forests. Developments in Hydrobiology 20. Dr. W. Junk Publishers, The Hague, pp. 89–109.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. Adv. Mar. Biol. 40, 81–251.

Kenyon, R.A., Loneragan, N.R., Hughes, J.M., 1995. Habitat type and light affect sheltering behaviour of juvenile tiger prawns (*Penaeus esculentus* Haswell) and success rates of fish predators. J. Exp. Mar. Biol. Ecol. 192, 87–105.

Kenyon, R.A., Loneragan, N.R., Manson, F.J., Vance, D.J., Venables, W.N., 2004. Allopatric distribution of juvenile red-legged banana prawns (*Penaeus indicus* H. Milne Edwards, 1837) and juvenile white banana prawns (*Penaeus merguiensis* De Man, 1888), and inferred extensive migration, in the Joseph Bonaparte Gulf, northwest Australia. J. Exp. Mar. Biol. Ecol. 309, 79–108.

King, R.J., Wheeler, M.D., 1985. Composition and geographic distribution of mangrove macroalgal communities in South Wales. Proc. Linn. Soc. N.S.W. 108, 97–117.

Kirton, L.G., 1995. Habitat and host associations of *Coptotermes* (Isoptera: Rhinotermitidae) in Peninsular Malaysia. Ph.D. Thesis. University of London, UK.

Kirton, L.G., Azmi, M., 1996. The mangrove milkweed butterfly project. The Forest Research Institute Malaysia and Malaysian Nature Society join hands in conservation. Malay. Nat. 49, 24–27.

Kirton, L.G., Azmi, M., 2000. Conservation of the mangrove tiger butterfly, *Danaus affinis* (Lepidoptera: Nymphalidae), in Kuala Selangor Nature Park. In: Insect Diversity and Conservation in the Tropics. Conference on Forestry and Forest Products (CFFPR) Series, Kuala Lumpur, 2–3 October 2000, p. 14.

Kirton, L.G., Azmi, M., 2004. Butterflies: tiger, tiger, burning bright. FRIM in Focus, April–June 2004, pp. 12–13.

Kito, K., Aryuthaka, C., 2006. New mouthless nematode of the genus *Parastomonema* Kito, 1989 (Nematoda: Siphonolaimidae) from a mangrove forest on the coast of Thailand, and erection of the new subfamily Astomonematinae within the Siphonolaimidae. Zootaxa 1177, 39–49.

Kneib, R.T., 1997. The role of tidal marshes in the ecology of estuarine nekton. Oceanogr. Mar. Biol. Annu. Rev. 35, 163–220.

Kondalarao, B., 1984. Distribution of meiobenthic harpacticoid copepods in Gautami Godavari estuarine system. Indian J. Mar. Sci. 13, 80–84.

Kondalarao, B., Raman-Murty, K.V., 1988. Ecology of intertidal meiofauna of the Kakinada Bay (Gautami-Godavari estuarine system), east coast of India. Indian J. Mar. Sci. 17, 40–47.

Krishnamurthy, K., Sultan Ali, M.A., Prince Jeyaseelan, M.J., 1984. Structure and dynamics of the aquatic food web community with special reference of nematodes in mangrove ecosystems. Proc. Asian Symp. Mangrove Env. Manage. 1, 429–452.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediments. Limnol. Oceanogr. 51, 1557–1571.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Kruitwagen, G., Nagelkerken, I., Lugendo, B.R., Pratap, H.B., Wendelaar Bonga, S.E., 2007. Influence of morphology and amphibious life-style on the feeding ecology of the mudskipper *Periophthalmus argentilineatus*. J. Fish Biol. 71, 39–52.

Krumme, U., Liang, T.H., 2004. Tidal-induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in northern Brazil. Zool. Stud. 43, 404–414.

Kumar, D., 1979. Biology and flashing behaviour of *Pteroptyx tener* (Olivier) (Coleoptera, Lampyridae) at Kuala Selangor. B.Sc. Thesis. University of Malaya, Malaysia.

Laegdsgaard, P., Johnson, C., 2001. Why do juvenile fish utilise mangrove habitats? J. Exp. Mar. Biol. Ecol. 257, 229–253.

Laprise, R., Blaber, S.J.M., 1992. Predation by moses perch, *Lutjanus russelli*, and blue spotted trevally, *Caranx bucculentus,* on juvenile brown tiger prawn. *Penaeus esculentus*: effects of habitat structure and time of day. J. Fish Biol. 40, 627–635.

Lavery, S., Chan, T.Y., Tam, Y.K., Chu, D.H., 2004. Phylogenetic relationships and evolutionary history of the shrimp genus *Penaeus s.l.* derived from mitochondrial DNA. Mol. Phylogenet. Evol. 31, 39–49.

Layman, C.A., Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Ley, J.A., Nagelkerken, I., Serafy, J.E., 2006. Marine nurseries and effective juvenile habitats. Mar. Ecol. Prog. Ser. 318, 307–308.

Lebata, M.J.H.L., Primavera, J.H., 2001. Gill structure, anatomy and habitat of *Anodontia edulenta*: evidence of endosymbiosis. J. Shellfish Res. 20, 1273–1278.

Lee, S.Y., 1997. Potential trophic importance of faecal material of the mangrove sesarmine crab *Sesarma messa*. Mar. Ecol. Prog. Ser. 159, 275–284.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshwater Res. 49, 335–343.

Lee, S.Y., 2004. Relationship between mangrove abundance and tropical prawn production: a re-evaluation. Mar. Biol. 145, 943–949.

Lee S.Y., 2008. Mangrove macrobenthos: assemblages, services, and linkages. J. Sea Res., doi:10.1016/j.seares.2007.05.002, in press.

Lee, O.H.K., Williams, G.A., Hyde, K.D., 2001. The diets of *Littoraria ardouiniana* and *L. melanostoma* in Hong Kong mangroves. J. Mar. Biol. Ass. U.K. 81, 967–973.

Leh, M.U.C., Sasekumar, A., 1984. Feeding ecology of prawns in shallow waters adjoining mangrove shores. In: Proceedings of the Asian Symposium on Mangrove Environment—Research and Management. pp. 331–353.

Leh, M.U.C., Sasekumar, A., 1985. The food of sesarmid crabs in Malaysian mangrove forests. Malay. Nat. J. 39, 135–145.

Lever, R.J.A.W., 1952. A Malayan leaf-tying caterpillar from mangroves periodically submerged in sea-water. Entomol. Mon. Mag. 88, 95.

Limpus, C.J., Limpus, D.J., 2000. Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. Mar. Turtle Newslett. 89, 13–15.

Limpus, C.J., Chatto, R., 2004. Marine turtles. In: National Oceans Office Description of Key Species Groups in the Northern Planning Area. National Oceans Office, Hobart, Australia.

Lindquist, E.S., Carroll, C.R., 2004. Differential seed and seedling predation by crabs: impacts on tropical coastal forest composition. Oecologia 141, 661–671.

Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar. Biol. 130, 289–300.

Loneragan, N.R., Adnan, A.N., Connolly, R.M., Manson, F.J., 2005. Prawn landings and their relationship with the extent of mangroves and shallow waters in western peninsular Malaysia. Est. Coast. Shelf Sci. 63, 187–200.

Lugendo, B.R., Pronker, A., Cornelissen, I., de Groene, A., Nagelkerken, I., Dorenbosch, M., van der Velde, G., Mgaya, Y.D., 2005. Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. Aquat. Living Resour. 18, 149–158.

Lugendo, B.R., Nagelkerken, I., van der Velde, G., Mgaya, Y.D., 2006. The importance of mangroves, mud/sand flats and seagrass beds as feeding areas for juvenile fish in Chwaka Bay, Zanzibar: gut content and stable isotope analysis. J. Fish Biol. 69, 1639–1661.

Lugendo, B.R., de Groene, A., Cornelissen, I., Pronker, A., Nagelkerken, I., van der Velde, G., Mgaya, Y.D., 2007a. Spatial and temporal variation in fish community structure of a marine embayment in Zanzibar, Tanzania. Hydrobiologia 586, 1–16.

Lugendo, B.R., Nagelkerken, I., Kruitwagen, G., van der Velde, G., Mgaya, Y.D., 2007b. Relative importance of mangroves as feeding habitat for fish: a comparison between mangrove habitats with different settings. Bull. Mar. Sci. 80, 595–607.

Luiselli, L., Akani, G.C., 2002. An investigation into the composition, complexity and functioning of snake communities in the mangroves of south-eastern Nigeria. Afr. J. Ecol. 40, 220–227.

Lyle, J.M., 1987. Observation on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzoryensis* (Whitley) from northern Australia. Aust. J. Mar. Freshwater Res. 38, 701–710.

Macia, A., Abrantes, K.G.S., Paula, J., 2003. Thorn fish *Terapon jarbua* (Forskål) predation on juvenile white shrimp *Penaeus indicus* (H. Milne Edwards) and brown shrimp *Metapenaeus monoceros* (Fabricius): the effect of turbidity, prey density, substrate type and pneumatophore density. J. Exp. Mar. Biol. Ecol. 291, 29–56.

Macintosh, D.J., Ashton, E.C., 2002. A review of mangrove biodiversity conservation and management. Final Report 10/06/2002. Centre for Tropical Ecosystems Research, University of Aarhus, Denmark. http://mit.biology.au.dk/cenTER/MCB_Files/2002_Review_WB_MCB_Final.pdf. Accessed: 26 February 2007.

Macnae, W., 1974. Mangrove Forests and Fisheries. FAO, Rome.

Magnusson, W.E., 1980. Habitat required for nesting by *Crocodylus porosus* (Reptilia: Crocodilidae) in northern Australia. Aust. Wildl. Res. 7, 149–156.

Makowski, C., Seminoff, J.A., Salmon, M., 2005. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida. Mar. Biol. 148, 1432–1793.

Manickchand-Heileman, S., Arreguín-Sánchez, F., Lara-Domínguez, A., Soto, L.A., 1998. Energy flow and network analysis of Terminos Lagoon, SW Gulf of Mexico. J. Fish Biol. 53, 179–197.

Manson, F.J., Loneragan, N.R., Skilleter, G.A., Phinn, S.R., 2005. An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. Oceanogr. Mar. Biol. Annu. Rev. 43, 483–513.

Martin, R.A., 2005. Conservation of freshwater and euryhaline elasmobranchs: a review. J. Mar. Biol. Ass. U.K. 85, 1049–1073.

Martosubroto, P., Naamin, N., 1977. Relationship between tidal forests and commercial shrimp production in Indonesia. Mar. Res. Indonesia 18, 81–86.

Meager, J.J., 2003. Microhabitat distribution of juvenile banana prawns (*Penaeus merguiensis*) and processes affecting their distribution and abundance. Ph.D. Thesis. Queensland University of Technology, Australia.

Meager, J.J., Vance, D.J., Williamson, I., Loneragan, N.R., 2003. Microhabitat distribution of juvenile *Penaeus merguiensis* de Man and other epibenthic crustaceans within a mangrove forest in subtropical Australia. J. Exp. Mar. Biol. Ecol. 294, 127–144.

Meager, J.J., Williamson, I., Loneragan, N.R., Vance, D.J., 2005. Habitat selection of juvenile banana prawns, *Penaeus merguiensis* de Man: testing the roles of habitat structure, predators, light phase and prawn size. J. Exp. Mar. Biol. Ecol. 324, 89–98.

Medway, L., Wells, D.R., 1976. The Birds of the Malay Peninsula, vol. 5. H.F. & G. Witherby, London.

Melville, A.J., Connolly, R.M., 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136, 499–507.

Metcalfe, K.N., Glasby, C.J. Diversity of Polychaeta (Annelida) and other worm taxa in mangrove habitats of Darwin Harbour, northern Australia. J. Sea Res., in press.

Metz, T.L., 2004. Factors influencing Kemp's ridley sea turtle (*Lepidochelys kempii*) distribution in nearshore waters and implications for management. Ph.D. Thesis. Texas A&M University, USA.

Meynecke, J.-O., Lee, S.Y., Duke, N.C., Warnken, J., 2007. Relationships between estuarine habitats and coastal fisheries in Queensland, Australia. Bull. Mar. Sci. 80, 773–793.

Meziane, T., Sanabe, M.C., Tsuchiya, M., 2002. Role of fiddler crabs of a subtropical intertidal flat on the fate of sedimentary fatty acids. J. Exp. Mar. Biol. Ecol. 270, 191–201.

Micheli, E., 1993. Feeding ecology of mangrove crabs in north eastern Australia—mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. J. Exp. Mar. Biol. Ecol. 171, 165–186.

Micheli, E., Gherardi, F., Vannini, M., 1991. Feeding and burrowing ecology of two East African mangrove crabs. Mar. Biol. 111, 247–254.

Miller, L.R., Paton, R., 1983. *Cryptotermes* in mangroves in the Northern Territory (Isoptera: Kalotermitidae). J. Aust. Entomol. Soc. 22, 189–190.

Minello, T.J., Zimmerman, R.J., 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated Spartina structure on predation rates. J. Exp. Mar. Biol. Ecol. 72, 211–231.

Minello, T.J., Zimmerman, R.J., Martinez, E.X., 1987. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: effects of turbidity and substratum on predation rates. Fish. Bull. U.S. 85, 59–70.

Minello, T.J., Able, K.W., Weinstein, M.P., Hays, C.G., 2003. Saltmarshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar. Ecol. Prog. Ser. 246, 39–59.

Mohan, P.C., Sreenivas, N., 1998. Diel variations in zooplankton populations in mangrove ecosystem at Gaderu canal, southeast coast of India. Indian J. Mar. Sci. 27, 486–488.

Montoya, R.V., Thorson, T.B., 1982. The bull shark (*Carcharhinus leucas*) and largetooth sawfish (*Pristis perotteti*) in Lake Bayano, a tropical man-made impoundment in Panama. Env. Biol. Fish. 7, 341–347.

Moore, P.G., 2002. Mammals in intertidal and maritime ecosystems: Interactions, impacts and implications. Oceanogr. Mar. Biol. 40, 491–608.

Moriarty, D.J.W., Barclay, M.C., 1981. Carbon and nitrogen content of food and the assimilation efficiencies of penaeid prawns in the Gulf of Carpentaria. Aust. J. Mar. Freshwater Res. 32, 245–251.

Morrissey, J.F., Gruber, S.H., 1993. Habitat selection by juvenile lemon sharks, Negaprion brevirostris. Env. Biol. Fish. 38, 311–319.

Morton, B.S., 1976. The biology and functional morphology of the Southeast Asian mangrove bivalve, *Polymesoda* (*Gelonia*) *erosa* (Solander 1786) (Bivalvia: Corbiculidae). Can. J. Zool. 54, 482–500.

Motuyang, C.P., 1994. Ecological studies of fireflies (*Pteroptyx tener*) in Kuala Selangor. B.Sc. Thesis. Universiti Putra, Malaysia.

Mumby, P.J., 2006. Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. Biol. Conserv. 128, 215–222.

Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C.C., Llewellyn, G., 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427, 533–536.

Murphy, D.H., 1965. *Deboutevillea marina* n. gen., n. sp., (Collembola, Sminthuridae) from the inter-tidal zone of Singapore. Bull. Nat. Mus. Singapore 33, 31–34.

Murphy, D.H., 1989. Three new species of nymphuline moths from Singapore mangroves provisionally attributed to *Eristena* Warren (Lepidoptera: Pyralidae). Raffles Bull. Zool. 37, 142–159.

Murphy, D.H., 1990. The natural history of insect herbivory on mangrove trees in and near Singapore. Raffles Bull. Zool. 38, 119–203.

Nada, B., Kirton, L.G., 2004. The secret life of fireflies. IRBM Updates 3, 2–4.

Nagelkerken, I., 2007. Are non-estuarine mangroves connected to coral reefs through fish migration? Bull. Mar. Sci. 80, 595–607.

Nagelkerken, I., van der Velde, G., 2002. Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? Mar. Ecol. Prog. Ser. 245, 191–204.

Nagelkerken, I., van der Velde, G., 2003. Connectivity between coastal habitats of two oceanic Caribbean islands as inferred from ontogenetic shifts by coral reef fishes. Gulf Caribb. Res. 14, 43–59.

Nagelkerken, I., van der Velde, G., 2004a. Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? Mar. Ecol. Prog. Ser. 274, 143–151.

Nagelkerken, I., van der Velde, G., 2004b. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. Mar. Ecol. Prog. Ser. 274, 153–159.

Nagelkerken, I., Faunce, C.H., 2007. Colonisation of artificial mangroves by reef fishes in a marine seascape. Est. Coast. Shelf Sci. 75, 417–422.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., Cocheret de la Morinière, E., van der Velde, G., 2000a. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar. Ecol. Prog. Ser. 194, 55–64.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., Cocheret de la Morinière, E., van der Velde, G., 2000b. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar. Ecol. Prog. Ser. 202, 175–192.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T., Den Hartog, C., 2000c. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Est. Coast. Shelf Sci. 51, 31–44.

Nagelkerken, I., Kleijnen, S., Klop, T., van den Brand, R.A.C.J., Cocheret de la Morinière, E., van der Velde, G., 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar. Ecol. Prog. Ser. 214, 225–235.

Nagelkerken, I., Roberts, C.M., van der Velde, G., Dorenbosch, M., van Riel, M.C., Cocheret de la Morinière, E., Nienhuis, P.H., 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Mar. Ecol. Prog. Ser. 244, 299–305.

Nagelkerken, I., van der Velde, G., Verberk, W.C.E.P., Dorenbosch, M., 2006. Segregation along multiple resource axes in a tropical seagrass fish community. Mar. Ecol. Prog. Ser. 308, 79–89.

Nallakumar, K.A., 1999. Twinkle Twinkle Fireflies. FRIM in Focus, October 1999, pp. 12–13.

Nallakumar, K.A., 2002. Management and conservation of fireflies in Peninsular Malaysia. Ph.D. Thesis. University of London, UK.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke, C., Lubchenco, J., Moony, H., Troell, M., 2000. Effect of aquaculture on world fish supplies. Nature 405, 1017–1024.

Netto, S.A., Gallucci, F., 2003. Meiofauna and macrofauna communities in a mangrove from the Island of Santa Catarina, South Brazil. Hydrobiologia 505, 159–170.

Ng, P.K.L., Sivasothi, N., 2002. A Guide to the Mangroves of Singapore. Raffles Museum of Biodiversity Research, second ed. National University of Singapore & Singapore Science Centre, Singapore.

Nicholas, W.L., Elek, J.A., Stewart, A.C., Marples, T.G., 1991. The nematode fauna of a temperate Australian mangrove mudflat; it population density, diversity and distribution. Hydrobiologia 209, 13–27.

Nijman, V., 2000. Geographic distribution of ebony leaf monkey *Trachypithecus auratus* (E. Geoffroy Saint-Hilaire, 1812) (Mammalia: Primates: Cercopithecidae). Contr. Zool. 69, 157–177.

Nisbet, I.C.T., 1968. The utilization of mangroves by Malayan birds. Ibis 110, 348–352.

Nixon, S.W., 1980. Between coastal marshes and coastal waters—a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity. In: Hamilton, P., MacDonald, K.B. (Eds.), Estuarine and Wetland Processes. Plenum Press, New York, pp. 437–525.

Nordhaus, I., 2004. Feeding ecology of the semi-terrestrial crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in a mangrove forest in northern Brazil. Contribution No. 18. Centre for Tropical Marine Ecology, Bremen, Germany.

Nordhaus, I., Wolff, M., Diele, K., 2005. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Est. Coast. Shelf Sci. 67, 239–250.

Noske, R., 1995. Ecology of mangrove forest birds in Peninsular Malaysia. Ibis 137, 250–263.

Noske, R., 1996. Abundance, zonation, and foraging ecology of birds in mangroves of Darwin Harbour, Northern Territory. Wildl. Res. 23, 443–474.

Nybakken, J.W., 1997. Marine Biology: An Ecological Approach, fourth ed. Addison Wesley Longman, Inc., Menlo Park, California.

Odum, W.E., Heald, E.J., 1972. The detritus-based food web of an estuarine mangrove community. Bull. Mar. Sci. 22, 671–737.

Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), Estuarine Research. Academic Press, New York, pp. 265–286.

Offenberg, J., Havanon, S., Aksornkoae, S., Macintosh, D.J., Nielsen, M.G., 2004a. Observations on the ecology of weaver ants (*Oecophylla smaragdina* Fabricius) in a Thai mangrove ecosystem and their effect on herbivory of *Rhizophora mucronata* Lam. Biotropica 36, 344–351.

Offenberg, J., Nielsen, M.G., Macintosh, D.J., Havanon, S., Aksornkoae, S., 2004b. Evidence that insect herbivores are deterred by ant pheromones. Proc. Royal Soc. Lond. B. 271 (Biology Letters Suppl. 6), S433–S435.

Ólafsson, E., 1995. Meiobenthos in mangrove areas in eastern Africa with emphasis on assemblage structure of free-living marine nematodes. Hydrobiologia 312, 47–57.

Ólafsson, E., Carlstrom, S., Ndaro, S.G.M., 2000. Meiobenthos of hypersaline tropical mangrove sediment in relation to spring tide inundation. Hydrobiologia 426, 57–64.

Omondi, J.G., Stark, J.R., 1996. In vitro carbohydrate digestibility tests in the Indian white shrimp, *Penaeus indicus*. Aquaculture 139, 315–328.

Pauly, D., 1985. Ecology of coastal and estuarine fishes in Southeast Asia: a Philippine case study. In: Yáñez-Arancibia, A. (Ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration. UNAM Press, Mexico, pp. 499–514.

Pauly, D., Ingles, J., 1986.In: The Relationship Between Shrimp Yields and Intertidal Vegetation (Mangrove) Areas: A Reassessment. IOC/FAO Workshop on Recruitment in Tropical Coastal Demersal Communities, IOC, UNESCO, Paris, Mexico, Ciudad de Carmen, pp. 227–284.

Pawlik, J.R., 1997. Fish predation on Caribbean reef sponges: an emerging perspective of chemical defenses. In: Proceedings of the Eighth International Coral Reef Symposium 2. pp. 1255–1258.

Pawlik, J.R., 1998. Coral reef sponges: do predatory fish affect their distribution? Limnol. Oceanogr. 43, 1396–1399.

Pawlik, J.R., McMurray, S.E., Henkel, T.P., 2007. Abiotic factors control sponge ecology in Florida mangroves. Mar. Ecol. Prog. Ser. 339, 93–98.

Pendoley, K., Fitzpatrick, J., 1999. Browsing on mangroves by green turtles in Western Australia. Mar. Turtle Newslett. 84, 10.

Pérez-Farfante, I., Kensley, B.F., 1997. Penaeoid and sergestoid shrimps and prawns of the world: keys and diagnoses for the families and genera. Mem. Mus. Natl. Hist. Nat. 175, 1–233.

Peterson, M.S., Comyns, B.H., Rakocinski, C.F., Fulling, G.L., 1999. Does salinity affect somatic growth in early juvenile Atlantic croaker, *Micropogonias undulatus* (L.)? J. Exp. Mar. Biol. Ecol. 238, 161–322.

Pineda, J.E.M., 2003. The contribution of mangrove outwelling to coastal food webs as a function of environmental settings. Ph.D. Thesis. University of Louisiana at Lafayette, USA.

Pittman, S.J., McAlpine, C.A., Pittman, K.M., 2004. Linking fish and prawns to their environment: a hierarchical landscape approach. Mar. Ecol. Prog. Ser. 283, 233–254.

Plaziat, J.C., 1984. Mollusc distribution in the mangal. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal—The Ecosystem of the Mangrove Forests. Developments in Hydrobiology 20. Dr. W. Junk Publishers, The Hague, pp. 111–143.

Por, F.D., 1977. The benthic copepods of the Sinai mangrove. Rapp. Comm. Int. Mer. Medit. 24, 87–89.

Por, F.D., 1984. Notes on the benthic copepods of the mangal ecosystem. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal—The Ecosystem of the Mangrove Forests. Developments in Hydrobiology 20. Dr. W. Junk Publishers, The Hague, pp. 67–70.

Por, F.D., Almeido Prado Por, M.S., Oliveira, E.C., 1984. The mangal of the estuary and lagoon system of Cananeia (Brazil). In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal—The Ecosystem of the Mangrove Forests. Developments in Hydrobiology 20. Dr. W. Junk Publishers, The Hague, pp. 211–228.

Primavera, J.H., 1997. Fish predation on mangrove-associated penaeids: the role of structures and substrate. J. Exp. Mar. Biol. Ecol. 215, 205–216.

Proches, S., Marshall, D.J., Ugrasen, K., Ramcharan, A., 2001. Mangrove pneumatophore arthropod assemblages and temporal patterns. J. Mar. Biol. Ass. U.K. 81, 545–552.

Proffitt, C.E., Devlin, D.J., 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove litter degradation rates. Mar. Ecol. Prog. Ser. 296, 209–218.

Qasim, S.Z., Kathiresan, K., 2005. Biodiversity of Mangrove Ecosystems. Hindustan Publishing Corporation, New Delhi.

Rahmat, A.A., 1996. Biological studies of the firefly *Pteroptyx tener* Olivier from Kampung Kuantan, Kuala Selangor. B.Sc. Thesis. University of Malaya, Malaysia.

Ray, S., Ulanowicz, R.E., Majee, N.C., Roy, A.B., 2000. Network analysis of a benthic food web model of a partly reclaimed island in the Sundarban mangrove ecosystem. Indian J. Biol. Syst. 8, 263–278.

Reice, S.R., Spira, Y., Por, F.D., 1984. Decomposition in the mangal of Sinai: the effect of spatial heterogeneity. In: Por, F.D., Dor, I. (Eds.), Hydrobiology of the Mangal—The Ecosystem of the Mangrove Forests. Developments in Hydrobiology 20. Dr. W. Junk Publishers, The Hague, pp. 193–199.

Ridd, P.V., 1996. Flow through animal burrows in mangrove creeks. Est. Coast. Shelf Sci. 43, 617–625.

Robertson, A.I., 1988. Abundance, diet and predators of juvenile banana prawns, *Penaeus merguiensis*, in a tropical mangrove estuary. Aust. J. Mar. Fresh. Res. 39, 467–478.

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., Duke, N.C., 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar. Biol. 96, 193–205.

Robertson, A.I., Duke, N.C., 1990a. Mangrove fish communities in tropical Australia: spatial and temporal patterns in densities, biomass and community structure. Mar. Biol. 104, 369–379.

Robertson, A.I., Duke, N.C., 1990b. Recruitment, growth and residence time of fishes in a tropical Australian mangrove system. Est. Coast. Shelf Sci. 31, 723–743.

Robertson, A.I., Blaber, S.J.M., 1992. Plankton, epibenthos and fish communities. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC. Coast. Est. Stud. 41, 173–224.

Rocha, R.M., Faria, S.B., Moreno, T.R., 2005. Ascidians from Bocas del Toro, Panama. I. Biodiversity. Caribb. J. Sci. 41, 600–612.

Rönnbäck, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol. Econ. 29, 235–252.

Rönnbäck, P., Troell, M., Kautsky, N., Primavera, J.H., 1999. Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. Est. Coast. Shelf Sci. 48, 223–234.

Rönnbäck, P., Macia, A., Almqvist, G., Schultz, L., Troell, M., 2002. Do penaeid shrimps have a preference for mangrove habitats? Distribution pattern analysis on Inhaca Island, Mozambique. Est. Coast. Shelf Sci. 55, 427–436.

Rooker, J.R., Dennis, G.D., 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. Bull. Mar. Sci. 49, 684–698.

Roque, S.M., 2007. Diversidad de Collembola (Hexapoda) asociados a *Rhizophora mangle* en manglares de Puerto Rico. M.Sc. Thesis. University of Puerto Rico, Puerto Rico.

Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99, 1–16.

Rützler, K., 1995. Low-tide exposure of sponges in a Caribbean mangrove community. PSZNI: Mar. Ecol. 16, 165–179.

Rützler, K., Feller, I.C., 1996. Caribbean mangrove swamps. Sci. Am. 274, 94–99.

Salick, J., Tho, Y.P., 1984. An analysis of termite faunae in Malayan rainforests. J. Appl. Ecol. 21, 547–561.

Salini, J.P., Blaber, S.J.M., Brewer, D.T., 1990. Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Mar. Biol. 105, 363–374.

Salini, J.P., Brewer, D.T., Blaber, S.J.M., 1998. Dietary studies on the predatory fishes of the Norman River Estuary, with particular reference to penaeid prawns. Est. Coast. Shelf Sci. 46, 837–847.

Santiapillai, C., de Silva, M., 2001. Status, distribution and conservation of crocodiles in Sri Lanka. Biol. Conserv. 97, 305–318.

Sarpedonti, V., Sasekumar, A., 1996. The abundance of diatom species on a low shore mangrove forest, Sementa Malaysia. Wallaceana 77, 21–26.

Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. J. Anim. Ecol. 43, 51–69.

Sasekumar, A., 1994. Meiofauna of a mangrove shore on the west coast of peninsular Malaysia. Raffles Bull. Zool. 42, 901–915.

Sasekumar, A., Ong, T.L., Thong, K.L., 1984. Predation of mangrove fauna by marine fishes. In: Soepadmo, E., Rao, A.N., Macintosh, D.J. (Eds.), Proc. Asian Symp. Mangrove Env. Res. Manage, University of Malaya and UNESCO, pp. 378–384.

Schmid, J.R., 2000. Activity patterns and habitat associations of Kemp's Ridley Turtles, *Lepidochelys kempii*, in the coastal waters of the Cedar Keys, Florida. Ph.D. Thesis. University of Florida, USA.

Schrijvers, J., Vincx, M., 1997. Cage experiments in an East African mangrove forest: a synthesis. J. Sea Res. 38, 123–133.

Schrijvers, J., Okondo, J., Steyaert, M., Vincx, M., 1995. Influence of epibenthos on meiobenthos of the *Ceriops tagal* mangrove sediment at Gazi Bay, Kenya. Mar. Ecol. Prog. Ser. 128, 247–259.

Schrijvers, J., Camargo, M.G., Pratiwi, R., Vincx, M., 1998. The infaunal macrobenthos under East African *Ceriops tagal* mangroves impacted by epibenthos. J. Exp. Mar. Biol. Ecol. 222, 175–193.

Serafy, J.E., Faunce, C.H., Lorenz, J.L., 2003. Mangrove shoreline fishes of Biscayne Bay, Florida. Bull. Mar. Sci. 72, 161–180.

Sheaves, M.J., 1998. Spatial patterns in estuarine fish faunas in tropical Queensland: a reflection of interaction between long-term physical and biological processes. Mar. Freshwater Res. 49, 31–40.

Sheaves, M., 2005. Nature and consequences of biological connectivity in mangrove systems. Mar. Ecol. Prog. Ser. 302, 293–305.

Sheaves, M., Molony, B., 2000. Short-circuit in the mangrove food chain. Mar. Ecol. Prog. Ser. 199, 97–109.

Sheaves, M., Baker, R., Johnston, R., 2006. Marine nurseries and effective juvenile habitats: an alternative view. Mar. Ecol. Prog. Ser. 318, 303–306.

Sheridan, P.F., 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. Bull. Mar. Sci. 50, 21–39.

Sheridan, P., Hays, C., 2003. Are mangroves nursery habitat for transient fishes and decapods. Wetlands 23, 449–458.

Shulman, M.J., 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66, 1056–1066.

Simpfendorfer, C.A., Milward, N.E., 1993. Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ. Biol. Fish. 37, 337–345.

Simpfendorfer, C.A., Heupel, M.R., 2004. Assessing habitat use and movement. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Biology of Sharks and their Relatives. CRC Press, Boca Raton, pp. 247–268.

Singh, H.R., Sasekumar, A., 1994. Distribution and abundance of marine wood borers on the west coast of peninsular Malaysia. Hydrobiologia 285, 111–121.

Sivasothi, N., 2000. Niche preferences of tree-climbing crabs in Singapore mangroves. Crustaceana 73, 25–38.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131, 1–7.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannick, N.T., Cocheret de la Morinière, E., van der Velde, G., 1997. Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). J. Exp. Mar. Biol. Ecol. 215, 35–48.

Smith, B.D., Braulik, G., Strindberg, S., Ahmed, B., Mansur, R., 2006. Abundance of irrawaddy dolphins (*Orcaella brevirostris*) and ganges river dolphins (*Platanista gangetica gangetica*) estimated using concurrent counts made by independent teams in waterways of the Sundarbans mangrove forest in Bangladesh. Mar. Mammal Sci. 22, 527–547.

Smith, T.J., Chan, H.T., McIvor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical tidal forests from three continents. Ecology 70, 146–151.

Smith, T.J., Boto, K.G., Frusher, S.D., Giddins, R.L., 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Est. Coast. Shelf Sci. 33, 419–432.

Somerfield, P.J., Gee, J.M., Aryuthaka, C., 1998. Meiofaunal communities in a Malaysian mangrove forest. J. Mar. Biol. Ass. U.K. 78, 717–732.

Somerfield, P.J., Warwick, R.M., Moens, T., 2005. Chapter 6: Meiofauna techniques. In: Eleftheriou, A., McIntyre, A. (Eds.), Methods for the Study of Marine Benthos. third ed. Blackwell Science Ltd., Oxford, pp. 229–272.

Spalding, M.D., 1998. Patterns of biodiversity in coral reefs and mangroves: global and local scales. Ph.D. Thesis. University of Cambridge, U.K.

Spiegelberger, T., Ganslosser, U., 2005. Habitat analysis and exclusive bank feeding of the Antillean manatee (*Trichechus manatus manatus* L. 1758) in the Coswine Swamps of French Guiana, South America. Trop. Zool. 18, 1–12.

Staples, D.J., 1980. Ecology of juvenile and adolescent banana prawns, *Penaeus merguiensis*, in mangrove estuary and adjacent off-shore area Gulf Carpentaria. II. Emigration, population structure and growth of juveniles. Aust. J. Mar. Freshwater Res. 31, 653–665.

Staples, D.J., Vance, D.J., 1979. Effects of changes in catchability on sampling of juvenile and adolescent banana prawns, *Penaeus merguiensis* de Man. Aust. J. Mar. Freshwater Res. 30, 511–519.

Staples, D.J., Vance, D.J., 1986. Emigration of juvenile banana prawns *Penaeus merguiensis* from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 27, 239–252.

Staples, D.J., Vance, D.J., Heales, D.S., 1985. Habitat requirements of juvenile penaeid prawns and their relationship to offshore fisheries. In: Rothlisberg, P.C., Hill, B.J., Staples, D.J. (Eds.), Second Australian National Prawn Seminar, Kooralbyn, Queensland. CSIRO, Australia, pp. 47–54.

Stieglitz, T., Ridd, P., Muller, P., 2000. Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. Hydrobiologia 421, 69–76.

Storr, G.M., Smith, L.A., Johnstone, R.E., 1986. Snakes of Western Australia. Western Australian Museum, Perth.

Sutherland, J.P., 1980. Dynamics of the epibenthic community on roots of the mangrove *Rhizophora mangle*, at Bahía de Buche, Venezuela. Mar. Biol. 58, 75–84.

Tanaka, J., Chihara, M., 1988. Macroalgal flora in mangrove brackish area of east Indonesia. In: Ogina, K., Chihara, M. (Eds.), Biological System of Mangroves. Ehime University, Japan, pp. 21–34.

Thayer, G.W., Colby, D.R., Hettler Jr., W.F., 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. Mar. Ecol. Prog. Ser. 35, 25–38.

Tho, Y.P., 1992. Termites of Peninsular Malaysia. In: Kirton, L.G. (Ed.), Malayan Forest Records No. 36. Forest Research Institute Malaysia, Kuala Lumpur.

Thollot, P., 1992. Importance of mangroves for Pacific reef fish species, myth or reality? Proceedings of the Seventh International Coral Reef Symposium 2. pp. 934–941.

Thong, K.L., Sasekumar, A., 1984. The trophic relationships of the fish community of the Angsa Bank, Selangor, Malaysia. In: Proc. Asian Symp. Mangrove Environ. Res. Manage. pp. 385–399.

Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neoepisesarma versicolor*) offered different food sources. Est. Coast. Shelf Sci. 65, 213–222.

Turner, R.E., 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Trans. Am. Fish. Soc. 106, 411–416.

UNEP-WCMC, 2007. Painted terrapin—*Callagur borneoensis*. http://www.unep-wcmc.org.

Valdés-Muñoz, E., Mochek, A.D., 2001. Behavior of marine fishes of the Cuban shelf. In: Claro, R., Lindeman, K.C., Parenti, L.R. (Eds.), Ecology of the Marine Fishes of Cuba. Smithsonian Institution Press, Washington, DC, pp. 73–114.

van Soest, R.M.W., 1994. Demosponge distribution patterns. In: van Soest, R.W.M., van Kempen, T.M.B., Braekman, J.C. (Eds.), Sponges in Time and Space. Balkema, Rotterdam.

Vance, D.J., Haywood, M.D.E., Staples, D.J., 1990. Use of a mangrove estuary as a nursery area for postlarval and juvenile banana prawns, *Penaeus merguiensis* de Man, in northern Australia. Est. Coast. Shelf Sci. 31, 689–701.

Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., Pendrey, R.C., 1996. How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia. Mar. Ecol. Prog. Ser. 131, 115–124.

Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., 1998. Seasonal and annual variation in abundance of postlarval and juvenile banana prawns *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Australia: a six year study. Mar. Ecol. Prog. Ser. 163, 21–36.

Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., Pendrey, R.C., 2002. Distribution of juvenile penaeid prawns in mangrove forests in a tropical Australian estuary, with particular reference to *Penaeus merguiensis*. Mar. Ecol. Prog. Ser. 228, 165–177.

Vanhove, S., Vincx, M., Vangansbeke, D., Gijselinck, W., Schram, D., 1992. The meiobenthos of 5 mangrove vegetation types in Gazi Bay, Kenya. Hydrobiologia 247, 99–108.

Vega-Cendejas, M.E., Arreguín-Sánchez, F., 2001. Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula, Mexico. Ecol. Model. 137, 119–133.

Verweij, M.C., Nagelkerken, I., de Graaf, D., Peeters, M., Bakker, E.J., van der Velde, G., 2006a. Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Mar. Ecol. Prog. Ser. 306, 257–268.

Verweij, M.C., Nagelkerken, I., Wartenbergh, S.L.J., Pen, I.R., van der Velde, G., 2006b. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, Haemulon flavolineatum. Mar. Biol. 149, 1291–1299.

Waddell, B., Pawlik, J.R., 2000. Defenses of Caribbean sponges against invertebrate predators: II. Assays with sea stars. Mar. Ecol. Prog. Ser. 195, 133–144.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Walton, M.E., Le Vay, L., Lebata, J.H., Binas, J., Primavera, J.H., 2007. Assessment of the effectiveness of mangrove rehabilitation using exploited and non-exploited indicator species. Biol. Conserv. 138, 180–188.

Ward, P., 1968. Origins of the avifauna of urban and suburban Singapore. Ibis 110, 239–255.

Warren, J.H., Underwood, A.J., 1986. Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. J. Exp. Mar. Biol. Ecol. 102, 223–225.

Wassenberg, T.J., Hill, B.J., 1993. Diet and feeding behaviour of juvenile and adult banana prawns (*Penaeus merguiensis* de Man) in the Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 94, 287–295.

Waterbury, J.B., Calloway, C.B., Turner, R.D., 1983. A cellulotytic nitrogen-fixing bacterium cultured from the gland of Deshayes in shipworms (Bivalvia, Teredinidae). Science 221, 1401–1403.

Webb, G.J.W., Messel, H., Magnusson, W., 1977. The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. Copeia 2, 238–249.

Webb, G.J.W., Buckworth, R., Manolis, S.C., 1983. *Crocodylus johnsoni* in the McKinlay River, N.T. VI. Nesting biology. Aust. Wildl. Res. 10, 607–637.

Webb, S.R., Kneib, R.T., 2002. Abundance and distribution of juvenile white shrimp *Litopenaeus setiferus* within a tidal marsh landscape. Mar. Ecol. Prog. Ser. 232, 213–223.

Webster, I.T., Ford, P., Tillman, P., 2005. Estimating nutrient budgets in tropical estuaries subject to episodic flows. Mar. Poll. Bull. 51, 165–173.

Wells, D.R., 1999. The Birds of the Thai-Malay Peninsula. Vol. 1, non-passerines, Academic Press, London.

Wells, F.E, 1984. Comparative distribution of macromolluscs and macrocrustaceans in a North-western Australian mangrove system. Aust. J. Mar. Freshwater Res. 35, 591–596.

Wells, F.E., 1990. Distribution of marine invertebrates in a Hong Kong mangrove, with emphasis on molluscs. In: Morton, B.S. (Ed.), Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, 1986, Hong Kong University Press, Hong Kong, pp. 783–793.

White, W.T., Potter, I.C., 2004. Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Mar. Biol. 145, 1023–1032.

Wilcox, T.P., Hill, M., DeMeo, K., 2002. Observations on a new two-sponge symbiosis from the Florida Keys. Coral Reefs 21, 198–204.

Williams, A.B., Deubler, E.E., 1968. A ten-year study of meroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesap. Sci. 9, 27–41.

Wilson, K.A., 1989. Ecology of mangrove crabs: predation, physical factors and refuge. Bull. Mar. Sci. 44, 263–273.

Wilson, S.K., Knowles, D.G., 1988. Australia's Reptiles. A Photographic Reference to the Terrestrial Reptiles of Australia. William Collins, Sydney.

Wolanski, E., Ridd, P., 1986. Tidal mixing and trapping in mangrove swamps. Est. Coast. Shelf Sci. 23, 759–771.

Wolanski, E., Mazda, Y., King, B., Gay, S., 1990. Dynamics, flushing and trapping in Hinchinbrook Channel, a giant mangrove swamp, Australia. Est. Coast. Shelf Sci. 31, 555–580.

Wolanski, E., Mazda, Y., Ridd, P., 1992. Mangrove hydrodynamics. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, D.C. Coast. Est. Stud. 41, 43–62.

Wolff, M., Koch, V., Isaak, V., 2000. A trophic flow model of the Caeté mangrove estuary (north Brazil) with considerations for the sustainable use of its resources. Est. Coast. Shelf Sci. 50, 789–803.

Wulff, J.L., 2005. Trade-offs in resistance to competitors and predators, and their effects on the diversity of tropical marine sponges. J. Anim. Ecol. 74, 313–321.

Yáñez-Arancibia, A. (Ed.), 1985. Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration. UNAM, Editorial Universitaria, Mexico.

Yoshiyasu, Y., 1984. A study of Thailand Nymphulinae (Lepidoptera, Pyralidae) (3) two new species of *Eristema* Warren. Tyô to Ga 35, 1–9.

Young, P.C., Carpenter, S.M., 1977. Recruitment of postlarval penaeid prawns to nursery areas in Moreton Bay, Queensland. Aust. J. Mar. Freshwater Res. 28, 745–773.

Zaidi, M.I., Yong, C.Y., 2004. Sychronous fireflies on berembang trees along Sungai Sepetang, Matang. In: Proceedings of the National Conference on Sustainable Management of Matang Mangroves, 100 years & Beyond (Biological Environment of Mangroves: Fauna), Ipoh, Malaysia, 5–8 October 2004, pp. 1–6.

Zhou, H., 2001. Effects of leaf litter addition on meiofaunal colonization of azoic sediments in a subtropical mangrove in Hong Kong. J. Exp. Mar. Biol. Ecol. 256, 99–121.

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Review

Faunal impact on vegetation structure and ecosystem function in mangrove forests: A review

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Abstract

The last 20 years witnessed a real paradigm shift concerning the impact of biotic factors on ecosystem functions as well as on vegetation structure of mangrove forests. Before this small scientific revolution took place, structural aspects of mangrove forests were viewed to be the result of abiotic processes acting from the bottom-up, while, at ecosystem level, the outwelling hypothesis stated that mangroves primary production was removed via tidal action and carried to adjacent nearshore ecosystems where it fuelled detrital based food-webs. The sesarmid crabs were the first macrofaunal taxon to be considered a main actor in mangrove structuring processes, thanks to a number of studies carried out in the Indo-Pacific forests in the late 1970s and early 1980s. Following these classical papers, a number of studies on Sesarmidae feeding and burrowing ecology were carried out, which leave no doubts about the great importance of these herbivorous crabs in structuring and functioning Old world ecosystems. Although Sesarmidae are still considered very important in shaping mangrove structure and functioning, recent literature emphasizes the significance of other invertebrates. The Ocypodidae have now been shown to have the same role as Sesarmidae in terms of retention of forest products and organic matter processing in New world mangroves. In both New and Old world mangroves, crabs process large amounts of algal primary production, contribute consistently to retention of mangrove production and as ecosystem engineers, change particle size distribution and enhance soil aeration. Our understanding of the strong impact of gastropods, by means of high intake rates of mangrove products and differential consumption of propagules, has changed only recently. The role of insects must also be stressed. It is now clear that older techniques used to assess herbivory rates by insects strongly underestimate their impact, both in case of leaf eating and wood boring species and that herbivorous insects can potentially play a strong role in many aspects of mangrove ecology. Moreover, researchers only recently realized that ant–plant interactions may form an important contribution to our understanding of insect–plant dynamics in these habitats. Ants seem to be able to relieve mangroves from important herbivores such as many insects and sesarmid crabs. It thus seems likely that ants have positive effects on mangrove performance.

Keywords: Herbivorous insect; Ant; Mangrove crab; Mangrove gastropod; Leaf damage; Propagule predation

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1. Introduction

During the past 20 years a paradigm shift has occurred concerning ideas about factors influencing mangrove forest structure and ecosystem dynamics. Prior to the 1980s, structural aspects of mangrove forests (e.g. species richness, plant distribution patterns, productivity, biomass) were viewed to be the result of abiotic processes acting from the bottom-up. Forces such as frequency and duration of tidal flooding, salinity, and sediment characteristics (nutrient availability, redox) were viewed as the primary drivers (see Smith, 1994 for a review). This view also existed at the ecosystem level. The outwelling hypothesis stated that mangrove primary production was removed via tidal action and carried to adjacent nearshore ecosystems where it fuelled detrital based food-webs (Odum, 1971; Odum and Heald, 1972,1975).

In the late 1970s and early 1980s a number of studies appeared indicating that biotic factors were important to shape mangrove forests vegetation structure and ecological processes occurring in them. Working in Florida, Beever et al. (1979) demonstrated that herbivory by the arboreal grapsid crab, *Aratus pisonii* (H. Milne Edwards), played a role in the energy flow of mangroves and that export of material via crab biomass could be significant. In Australia, Robertson (1986) demonstrated that crabs had significant impacts on energy flow and export from mangroves, while Smith (1987) showed that, by consuming mangrove propagules, crabs could influence forest structure. Subsequent experimental work revealed that burrowing by crabs had significant effects on sediment chemistry and forest productivity (Smith et al., 1991).

The foundation for the idea of crabs as ecosystem engineers had just been laid when other invertebrate taxa, such as molluscs and insects, went on the stage. In fact, Bouillon et al. (2002a,b), using carbon and nitrogen stable isotope signatures, showed that molluscs' overall consumption of mangrove litter in some Indo-Pacific mangrove forests, and consequent contribution in nutrient dynamics, can be much higher than that of sesarmid crabs. Molluscs can reach an astonishingly high biomass in mangroves and they occupy very different levels of the ecosystem food web. While gastropods contribute to entrap primary production within the system, both grazing fallen leaves and consuming mud (mainly composed by mangrove litter), bivalves are efficient filter feeders, able to capture suspended particles of various origins (Plaziat, 1984; Kathiresan and Bingham, 2001).

In virtually all forest ecosystems, insects have a significant impact on tree growth rate and form, survivorship, reproductive output and forest ecology (Schowalter, 1986; Crawley, 1989), however, the impact by insects on mangroves has been considered of minor importance compared to other types of forests (Macnae, 1968). However, an increasing focus on mangrove herbivory has shown that the situation is not different in mangroves. Being dominated by trees, mangroves forests are similar to terrestrial forests in many ways, this being especially so for canopy fauna such as insects. In a thorough review, Burrows (2003) found no evidence that mangrove trees in general had lower levels of herbivory than tree species elsewhere, with any differences being attributable to individual species characteristics rather than a general feature of mangrove forests.

Among the insects, ants play an important ecological role. Their high abundance and the multitude of interactions they are engaged in make them important actors in ecosystem functioning (Wilson, 1959; Beattie, 1985; Hölldobler and Wilson, 1990). From terrestrial studies it is well documented that ants are able to protect plants against herbivores via their predatory and territorial behaviour (reviewed by Bronstein, 1998). Only few studies have dealt with mangrove ants. These suggest that densities may be lower than in terrestrial habitats, but still ants are among the most numerous groups of animals (Simberloff and Wilson, 1969; Clay and Andersen, 1996; Cogni et al., 2003; Dejean et al., 2003). The general picture that emerges from the present mangrove ant studies is that ants have a significant effect on the plant community via their interactions with herbivores. Moreover, some new and fascinating ant–plant protection interactions have been revealed in the mangrove (Offenberg, 2004). For example, Offenberg et al. (2006a) showed that ants indirectly, via their protection against leaf beetle folivory, protect mangrove trees against male crab grazing but not against grazing by female crabs.

The few examples sketched above show how macrofaunal assemblages were only recently considered of major importance in shaping mangrove ecosystem structure and function. The present paper is thus aiming to review the ecological role of the main actors among the faunal taxa, trying to depict what is now known and what we still need to clarify on the importance of biotic impacts on mangrove ecosystems.

2. Insects

2.1. Herbivorous insects in mangroves

2.1.1. Leaf-feeders

The most common forms of insect herbivory are leaf-feeding, wood-boring and flower/fruit/seed-feeding. Leaf-feeding has been most studied in mangroves and the dominant means of assessing this is to measure the amount of leaf area missing or being damaged from a sample of leaves collected from a tree. This discrete technique has been utilised in 20 separate studies in mangroves (reviewed in Burrows, 2003). However, because this method does not account for leaves that are entirely eaten or prematurely abscised because of high damage levels, it significantly underestimates the true level of leaf material lost to herbivores (Lowman, 1984; Landsberg, 1989; Landsberg and Ohmart, 1989; Aide, 1993; Hurley, 1995; Jackson, 1995; Burrows, 2003). Alternative methods of assessing leaf loss have shown that up to 13% of *Rhizophora stylosa* Griff. and 36% of *Avicennia marina* (Forsk.) Vierh. leaf material, can be lost to herbivores (Burrows, 2003), this being 2–5 times greater than estimates usually produced from discrete studies. Although the application of these alternative methods are more time-consuming, they do provide a very different picture of herbivore damage. Instances of mass defoliation events in mangroves (reviewed in Burrows, 2003) are treated as curiosities and are usually only reported anecdotally or in short note form. Three exceptions are from Ecuador (Gara et al., 1990), Hong Kong (Anderson and Lee, 1995) and Queensland, Australia (Duke, 2002), with the latter two including detailed studies of defoliation ‘events’ that lasted several years. Duke (2002) proposed that such events be considered as a potentially important ecological process and studied in more detail.

The mechanisms by which insects damage mangrove leaves also varies. In the study of Burrows (2003), leaf surface area missing or damaged only comprised one-third of leaf area damaged by insects, with leaf mines, galls and necrosis due to sap-feeders also major sources of leaf damage. Damage to apical buds and developing leaves can be substantial and in an Australian study of *R. stylosa*, loss of leaf material during the short development phase prior to unfurling from the stipules, was greater than what occurred for the entire lifetime for those leaves that did survive to full emergence (Burrows, 2003). Loss of these apical buds can also reduce reproductive output and leaf production rates, and alter the branching pattern of *Rhizophora* species (Onuf et al., 1977; Murphy, 1990; Anderson and Lee, 1995; Feller, 1995; Burrows, 2003). Insect feeding also causes the premature abscission of heavily damaged leaves. For both *A. marina* and *R. stylosa*, Burrows (2003) found that the amount of leaf area prematurely abscised because of insect damage was equal to or greater than that actually consumed by the insects themselves. Thus an assessment of actual herbivore damage to leaves requires an assessment of leaf area loss over time, other forms of leaf damage, loss of abscised intact leaf material and reduced leaf production.

2.1.2. Wood-borers

Studies of the ecological effect of insect wood-borers in mangroves are limited to those of Feller and Mathis (1997), Feller and McKee (1999) and Feller (2002). For Belizean *Rhizophora mangle* L. forests, these studies have shown that the amount of leaf area lost due to the feeding activities of wood-boring insects (which cause mortality of leaves distal to the point at which the branches are fed upon) was equal to or greater than that lost directly to leaf-feeding insects themselves. Conversely, at one site, Burrows (2003) found that through their destruction of the apical meristem of *R. stylosa* (and subsequent failure of the shoot to produce any new leaves), leaf-feeding herbivores caused greater mortality of woody shoots than wood-borers did. Thus, the mechanisms of herbivore damage are not always obvious and wood-boring may be an unexpected cause.

2.1.3. Effect of herbivory on reproductive output

Analogous to the situation for leaf production, the number of propagules a plant produces may be affected more by reallocation of resources to compensate for herbivore damage elsewhere on the plant, than by actual damage to propagules themselves. Although the degree of herbivore attack in both instances was unusually high, Anderson and Lee (1995) and Tong et al. (2003), showed that defoliation of *A. marina*, and artificial damage to *Kandelia candel* (L.) Druce, significantly reduced propagule production, thus making it a more important form of reduced reproductive output than predation upon the propagules that were actually produced.

Quantification of reduced growth rates and mangrove tree mortality due to herbivores is limited, even for events of mass defoliation. Ozaki et al. (1999) showed that scale insect infestation could cause mortality of *Rhizophora mucronata* Lam. saplings. Most commonly however, studies of mortality and reduced growth rate have been performed on propagules and seedlings. In a rapid global survey of mangrove pre-dispersal propagule predation, Farnsworth and Ellison (1997) found that insects were the most damaging herbivores. Onuf et al. (1977), Rabinowitz (1977), Robertson et al. (1990), Clarke (1992), Elster et al. (1999), Brook (2001), Minchinton and Dalby-Ball (2001) and Sousa et al. (2003) have all shown high frequencies and levels of insect predation (mainly beetles and caterpillars) upon mangrove propagules, though the subsequent impacts of this attack upon seedling growth and survival are variable.

Elster et al. (1999) found that caterpillars caused substantial mortality (up to 100% at some sites) of *Avicennia germinans* (L.) Stearn propagules and seedlings. Sousa et al. (2003) found that the boring of the scolytid beetle, *Coccotrypes rhizophorae* (Hopkins), into *R. mangle* propagules killed 72–89% of seedlings planted in closed canopy sites (but only 1–2% in adjacent light gaps). These beetles can seriously affect mangrove restoration efforts involving propagules (Kaly and Jones, 1998; Elster et al., 1999). The level of impact on propagules can depend on many factors apart from the amount of damage. These include where the damage occurs (internally boring insects are more damaging, Farnsworth and Ellison, 1997; Minchinton and Dalby-Ball, 2001) and the intertidal and micro-habitat position of the propagule (Robertson et al., 1990).

2.1.4. *Costs of herbivore damage*

Herbivorous insect impact in itself is often not directly related to the amount of damage caused and certain types and levels of damage may have no effect at all, thus the magnitude of the impact cannot be judged solely from the amount of damage measured. Burrows (2003) and Minchinton and Dalby-Ball (2001) provide mangrove examples of how small amounts of feeding on key parts of leaves and fruit respectively, can have much greater impacts than greater amounts of feeding on less important tissues. In *Rhizophora* for example, small amounts of herbivore damage to the apical buds has much greater effect on leaf survival and retention than larger amounts of damage to leaf lamina (Burrows, 2003).

The costs of anti-herbivore defences need to be weighed against the costs of plant material lost to herbivores. The comparison between *Avicennia* and *Rhizophora* leaves illustrated in Burrows (2003) provides an example. Leaves of *Rhizophora* (and indeed other Rhizophoraceae) are generally larger, thicker and heavier than those of *Avicennia* species, requiring more energy and investment in their construction. For instance, Burrows (2003) found *R. stylosa* leaves to, on average, cover more than twice as much surface area, to be 35% thicker and to have 34% more leaf mass per unit area, than *A. marina* leaves. Thus *Rhizophora* leaves may be more worth defending against herbivore attack than *Avicennia* leaves which would appear to be more expendable. Or put another way, *Avicennia* has a strategy of producing many leaves, each with less investment and thus tolerating high levels of damage, whereas *Rhizophora* produces fewer leaves with greater investment in each leaf. The true cost of herbivore attack is thus the energy lost to herbivore damage plus the energy invested in defending against such loss. Another difference between *Avicennia* and *Rhizophora* is the different ability to recover from damage. *Avicennia* has precocious leaf production and if a branch is damaged, many new sprouts soon form, whereas for *Rhizophora*, leaf production is confined to the apical meristem. If that is damaged, suppressed laterals may compensate but as shown by Burrows (2003), this is hardly sufficient, and loss of the apical meristem most commonly results in cessation of leaf production from that shoot, ultimately leading to its death. Thus the two species differ in their ability to recover from insect (and other forms of) damage. Taken together, the most important effect of herbivores on *Rhizophora* may be suppressed leaf production (an effect only detectable through measurement not observation) whereas the more visually obvious consumption of leaf material may be more important in species of *Avicennia*.

The literature in terrestrial forests contains many studies on the costs of anti-herbivore defences and how in times of resource-shortage, these defences may be foregone, rendering plants more susceptible to herbivore attack. This topic has only been addressed in a limited manner for mangroves. An interesting illustration of the point is provided by the observations of McKillup and McKillup (1997). They noted that the blind-your-eye mangrove, *Excoecaria agallocha* L., was rarely attacked by insects but that during a drought, many plants were severely insect attacked, except those who bordered the only remaining sources of fresh groundwater. The paper was only observational, no leaf chemistry was undertaken to support the observations, but it does illustrate the possibility that when stressed, the trees reduced investment in their anti-herbivore defenses, and were subsequently attacked and defoliated. In Sri Lanka, however, leaf herbivory by caterpillars affects 100% of *E. agallocha* leaves every year (pers. obs.). While anti-herbivores defences may decrease when under stress, trees may also respond to insect attack by altering the level of various chemical compounds in leaves that may act to deter insect herbivores. For example, leaf tannins are thought to decrease herbivore feeding activity. Anderson and Lee (1995) showed that although the tannin content of *A marina* leaves attacked by insects during a defoliation event, did not increase, the next cohort of leaves subsequently produced by the trees did have elevated tannin content. Tong et al. (2003) demonstrated that artificially damaged *K. candel* leaves subsequently showed altered leaf chemistry such as decreased nutrient and tannin levels. Although the value of reducing tannin levels is unclear, the decreased leaf nutrient content would be expected to reduce herbivore growth rates and may thus act as a deterrent. Neither study examined insect herbivore damage on leaves after the observed chemical changes, thus leaving the question as to the actual effectiveness of such chemical responses unresolved.

Resource availability can influence herbivore attack not just through anti-herbivore defences but through the attractiveness of plant material. Onuf et al. (1977) reported significantly higher levels of herbivore damage and lost leaf production of *R. mangle* at higher nutrient sites. Feller (1995) showed that herbivory on *R. mangle* trees artificially treated with P and NPK fertiliser significantly increased by some specialists, though not generalists, despite the increase in leaf phenolic compounds that accompanied the fertiliser treatments. Although herbivore damage rate increased, because leaf production rates of the fertilised trees also increased, the actual proportion of total potential leaf production did not differ between the treatments. This conflicts with the study of Onuf et al. (1977) where an increased rate of leaf production did not keep up with the increased rate of herbivory. However, Onuf et al. (1977) did not provide leaf nutrient content data so the relative degree of fertilisation between the two studies cannot be compared.

2.2. *Ants in mangroves*

Ants are numerous in terrestrial habitats and are probably the group of insects that has the highest ecological impact in many ecosystems since they can make up more than 10% of the faunal biomass (Wilson, 1959; Hölldobler and Wilson, 1990). They play an important role via their various interactions with plants. Disregarding leaf cutter and harvester ants, most ant–plant interactions are beneficial to plants. They include ants providing nutrients to plants, pollination, seed dispersal and protection against herbivory (Beattie, 1985). In return plants provide easily collectable food and/or hollow structures where the ants can nest (Beattie, 1985). Thus, despite indirect negative impacts from ants, such as the tending of herbivorous homopterans (Way, 1963), many plant species invest in strategies to attract ant partners and the net outcome in most cases is considered to be positive (Bronstein, 1998).

Most ants are ground dwelling and therefore face considerable problems getting established in the regularly flooded mangroves. Even so, they remain the most dominant insects in this habitat (Clay and Andersen, 1996; Dejean et al., 2003) both numerically and energetically (Simberloff and Wilson, 1969). The mangrove ant fauna is composed of terrestrial species as well as species endemic to mangroves. Though a few species have adapted to nest in the flooded sediment (Clay and Andersen, 1996; Nielsen, 1997a,b; Nielsen et al., 2003a,b), compared to terrestrial habitats, the species composition is skewed toward arboreal species (Clay and Andersen, 1996; Nielsen, 2000; Wetterer and O'hara, 2002; Cogni et al., 2003; Dejean et al., 2003). The predominant arboreal life style, though, may favor ant protection since ants are constrained to forage on plants.

2.2.1. *Ants impact on mangrove herbivores*

Mangrove ant studies have largely dealt with four major topics: (i) species surveys investigating distribution (Simberloff and Wilson, 1969; Cole, 1983b; Clay and Andersen, 1996; Veenakumari et al., 1997; Nielsen, 2000; Wetterer and O'hara, 2002; Cogni and Freitas, 2002; Dorou et al., 2002), (ii) nesting behaviour and adaptations to the mangrove environment (Cole, 1980; Nielsen, 1997a,b; Dejean et al., 2003; Nielsen et al., 2003a,b; Nielsen et al., 2006), (iii) ant community interactions (territoriality) (Cole, 1983a,b; Adams, 1994) and (iv) ant–plant interactions (Johnstone, 1985; Ozaki et al., 2000; Cogni and Freitas, 2002; Cogni et al., 2003; Dejean et al., 2003; Offenberg et al., 2004a,b; Offenberg et al., 2005, 2006a,b; Offenberg, 2007). A first approach to test for ant–plant protection is to artificially apply arthropod prey on plants and check for ant predation. Cogni and Freitas (2002) investigated the ant fauna on extrafloral nectary bearing *Hibiscus pernambucensis* Arruda in a mangrove in Brazil and found that out of 19 ant species 8 species attacked live termite baits. Similarly Cogni et al. (2003) found that 60% of artificial termite baits were detected by ants within 60 min on *H. pernambucensis* and on neighboring vegetation without extrafloral nectaries, in the same mangrove forest; this despite a higher ant occupancy frequency and mean number of ants on *H. pernambucensis* compared to the nearby plants. Attacked termites were detected after only 4 min on average. A second approach is to test if ants reduce present herbivore populations and if a reduction translates into reduced herbivory. Ozaki et al. (2000) provided compelling evidence of the reduction of a scale pest population (*Aulacaspis marina* Takagi and Williams) on *R. mucronata* by the ants *Monomorium floricola* (Jerdon) and *Paratrechina* sp. in a mangrove in Bali. On ant excluded saplings 90% of artificially introduced female scales survived a three day experiment while only 22% survived on plants foraged by ants. Offenberg et al. (2005) also found a significant reduction in the herbivore community on ant (*Oecophylla smaragdina* Fabr.) visited young *R. mucronata* trees compared to control trees without ants in a Thai mangrove. In contrast, the beneficial predatory arthropod guild was not significantly affected. In this case it was seen that the reduction in herbivore numbers resulted in significantly reduced herbivory levels on ant-trees caused by all the four major herbivores (Fig. 1 and Table 1).

A similar result was found on mature trees in the same area; ant associated trees experienced more than four times less foliovory than trees without ants, despite an overall damage of less than 3% leaf area loss. Also, damage levels within ant-trees were seen to be negatively correlated with ant densities (Offenberg et al., 2004a). The first published study on mangrove ant–plant interactions by Johnstone (1985) similarly found a trend for less foliovory on mangroves with *O.*

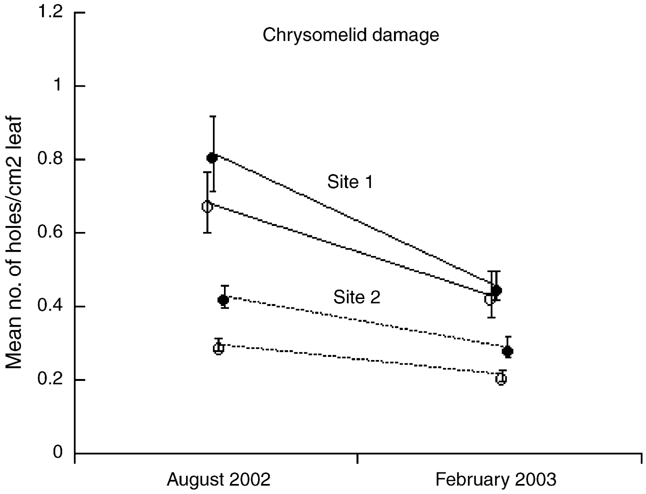

Fig. 1. The amount of damage caused by chrysomelid beetles on *R. mucronata* trees with and without *O. smaragdina* ants. Symbols show the tree mean no. of holes per cm^2 leaf area on ant (open symbols) and control trees (solid symbols) at site 1 (solid lines) and 2 (broken lines) at two surveys. At site 1, $N_{\text{ants}} = 7$ and $N_{\text{control}} = 8$ trees; at site 2, $N = 13$ trees in both groups. From Offenberg et al. (2005).

Table 1
Damage caused by three herbivores on *Rhizophora mucronata* trees with and without *Oecophylla smaragdina* ants

	Damage				Unit
	Ants		Control		
	Mean ± S.E.	*N* (trees)	Mean ± S.E.	*N* (trees)	
Tortricid	1.93 ± 1.07	20	10.01 ± 3.98	21	% Attacked shoots
Geometrid	0.40 ± 0.15	13	3.28 ± 1.43	13	% Leaves eaten
Sesarmid	0.25 ± 0.08	13	0.44 ± 0.12	13	% Eaten leaf area

Modified from Offenberg et al. (2005).

smaragdina ants on the Papuan coast, however, the difference between ant-trees and non-ant trees was not significant, leading Johnstone to conclude that ants were unable to protect mangroves. The insignificance, though, could have been caused by the pooling of leaves from different tree species. Hence, mangrove ants can reduce herbivore numbers and herbivore damage, however, reports on their effect on plant performance is scarce. One study have addressed this problem and found that ant associated trees with fewer herbivores and less folivory showed a marginally insignificant trend toward lower performance than control trees (Offenberg et al., 2005). Thus, reduced herbivory may not necessarily lead to increased plant performance since plants may compensate or even overcompensate in response to herbivory (Huhta et al., 2003). The positive effect by ants acting on the herbivore population and the herbivore damage level may also be counteracted by the indirect negative effects that ants may exert on their host plants via trophobiosis with herbivorous honeydew producing hemiptera and lycaenid larvae (Buckley, 1987) and via their nest building. In most cases, though, these effects are considered less significant than the positive effects from ants. For example, leaf nest building by *O. smaragdina* on *R. mucronata* reduced the longevity of the leaves used in the nest, but this effect was estimated to be 3–20-fold lower than the positive effect afforded via protection against foliovory (Offenberg et al., 2006b). Still lacking from this estimate, however, is the effect of sap sucking scale insects attended by the ants on these trees. At present, probably the best evidence of a positive effect by ants on plant performance is the study by Ozaki et al. (2000) which might have shown a considerable positive effect on plant survival if it had addressed this issue by prolonging the study period. Saplings in plantations with no ants experienced scale insect infestation levels (>200 females/leaf) resulting in the death of seedlings within 5 months with up to 70% mortality, whereas nearby natural mangroves with ants had almost no scale insects.

3. Crabs

3.1. Damage by herbivorous crabs

Although the vast majority of leaf-feeding crabs actually depends on leaf litter, some species colonising both New world and Indo-Pacific mangroves evolved a tree-climbing inhabit often coupled with an herbivorous feeding regime (Fratini et al., 2005). Among these climbers, one of the most studied is surely the sesarmid crab *Aratus pisonii*, in fact, is common in mangroves colonising both the Pacific and Atlantic tropical and sub-tropical coasts of the American continent and it is known to inhabit the mangrove canopy as adult and to rely mainly on fresh leaves (Warner, 1967; Beever et al., 1979; Erickson et al., 2003). *A. pisonii* removes the top layers of the leaves by scraping the leaf surface and, although its damage does not penetrate the entire leaf, can remove up to 30% of an individual leaf (Erickson et al., 2003). In Florida, the heavy impact due to the herbivory of this tree-climber within the stands dominated by *R. mangle* has been shown by Erickson et al. (2003), which observed that the percentage of damaged leaves can be up to 30–40% of the total leaves on the trees.

Even though the species diversity of tree-climbing crabs in the Indo-Pacific systems is undoubtedly high, comprising species belonging to at least two families and five genera (Fratini et al., 2005), reliable data on the impacts of their herbivorous habits are available only for *Parasesarma leptosoma*, a mangrove-climber colonising the whole East African coasts, from Kenya to South Africa (Vannini and Ruwa, 1994; Emmerson et al., 2003). In Kenya their average density can be about 200–300 crabs per mature *R. mucronata* tree, their preferred food source, and they can damage, by scraping the leaf-tissues with their claws, up to 50–60% of the fresh leaves of the canopies (Cannicci et al., 1996a,b). Since the damages operated by crabs feeding on fresh leaves are similar to the ones due to many herbivorous insects, their implications in terms of costs for the trees should be similar, but no experimental data exists on this topic and further work is indeed required to understand the scale of crab herbivory impact and the actual defences evolved by the plants themselves.

3.2. Retention of primary productivity within the ecosystem

Crabs are known to be the main agents responsible for the high leaf litter turnover rates in mangrove systems (Lee, 1998, 2008). Sesarmids are surely the main consumers of mangrove leaf litter along the Indo-Pacific region, but their influence is highly variable, thus broad generalizations about the extent of their impacts are difficult to draw (Table 2).

Although the role of sesarmid crabs in the leaf turnover of neotropical mangroves was never considered of primary importance, with the exception of the tree-climber *A. pisonii* (Beever et al., 1979) recent studies showed how this role of litter consumption is played by the ocypodid crabs of the genus *Ucides* (Table 2). Indeed, Twilley et al. (1997) pointed out that

Table 2
Mangrove litter consumption rates, as percentage of leaf litter production, recorded for mangrove crabs belonging to Neotropic and Indo-Pacific ecosystems

Region	Mangrove	Consumption rate (%)	Crabs	Crab family	Reference
Neotropic	*Rhizophora* sp.	81	*Ucides cordatus*	Ocypodidae	Nordhaus et al., 2006
Indo-Pacific	*Rhizophora* sp.	9	*Perisesarma (Chiromates) onychophorum*, *P. eumolpe*	Sesarmidae	Leh and Sasekumar (1985)
		>100	*Neoepisesarma* spp., *Perisesarma* (*Chiromantes*) spp.	Sesarmidae	Poovachiranon and Tantichodok (1991)
		28	*Perisesarma messa*	Sesarmidae	Robertson (1986)
	Ceriops sp.	71	*Perisesarma messa*, *Neosarmatium smithi*	Sesarmidae	Robertson and Daniel (1989)
	Bruguiera sp.	79	*Perisesarma messa*, *Neosarmatium fourmanoiri*	Sesarmidae	Robertson and Daniel (1989)
	Avicennia sp.	33	*Neosarmatium fourmanoiri*, *Parasesarma moluccensis*	Sesarmidae	Robertson and Daniel (1989)
		44	*Neosarmatium meinerti*	Sesarmidae	Emmerson and McGwynne (1992)
		>100	*Neosarmatium meinerti*	Sesarmidae	Olafsson et al. (2002)
	Kandelia sp.	57	*Perisesarma bidens*, *Parasesarma affinis*	Sesarmidae	Lee (1989)

Ucides occidentalis Ortmann leaf-burying behaviour affected the litter dynamics of Ecuadorian mangroves similarly to the high rates of leaf-burrowing known for Indo-Pacific sesarmids.

On the other hand, Indo-Pacific Ocypodidae are among the main consumers of another source of organic compounds, derived from microalgal and bacterial primary production. Crabs belonging to the genera *Uca* and *Dotilla* are known to ingest benthic, as well as periphytic (Hootsmans et al., 1993), bacteria and microalgae (France, 1998; Bouillon et al., 2002a), and proved capable of removing high rates of chlorophyll *a* and bacteria near the sediment (Kristensen and Alongi, 2006).

If the role of mangrove litter retention by crabs in maintaining the organic matter into the system is certain, their trophic role is still a matter of debate (see also Kristensen et al., 2008). Do they primarily consume the leaves they store in their burrows? Freshly senescent leaves of all mangrove species, i.e. what is commonly available for the crabs, are characterised by very low nutritional values, have a very high C/N ratio, up to 100, and high concentration of tannins, which interfere with protein digestion acting as feeding deterrents. Apart from these biochemical considerations, direct observations on feeding behaviour of Indo-pacific sesarmids (Kwok, 1999; Skov and Hartnoll, 2002) and studies comparing the stable isotope signature of mangrove leaves and sesarmid crabs (Bouillon et al., 2002a,b; Thongtham and Kristensen, 2005) show that they do not totally rely on leaf litter as a food source. These recent results lead to another unresolved question, what are the other sources of food for crabs?

3.3. Enrichment of mangrove organic production

Although crabs act as the major initial processors of mangrove leaf organic matter, their trophic dependence on this matter is probably less significant than is suggested by the data on removal. Although sesarmids and ocypodids can consume up to ~100% of the mangrove leaf litter of Old and New world mangroves, respectively, little is known about the fate of the organic matter they consume. Crabs' assimilation rate of the leaf litter is generally low (<50%), and about 60% of the dry mass of the material consumed is egested as faecal matter (Lee, 1993), resulting in high faecal rate production by crabs. As an example, Lee (1997) showed that *Perisesarma messa* Campbell, feeding on *R. stylosa* leafs in Australia, produced faecal material at a rate equivalent to about 24% of the leaf litter fall of the forest.

The physical and chemical conditions of mangrove leaf litter can change noticeably during the digestion process of crabs, and these changes can enhance the nutritional qualities of crabs faecal material, which is thus exploited by both small autochthonous and alloctonous benthic invertebrate consumers. In fact, Lee (1997) showed that *P. messa* faeces, at least 2 weeks old, were significantly richer in nitrogen, and less rich in tannins than unprocessed mangrove litter. As a result of these chemical changes, in laboratory experiments, the same faecal material proved to be a source of food of better quality than the mangrove litter for the benthic amphipod *Parhyallela* sp., attaining significantly higher mortality rates. More recently, Werry and Lee (2005) showed that mangrove organic matter is shredded to microscopic fragments of ~200 μm in size in the faeces of *Parasesarma erythrodactyla* (Greenwood and Fielder). The faecal matter was colonised by bacteria, which proved to be ~70× more abundant than on whole leaf litter undergoing normal decomposition. Moreover, a rise in nitrogen content that was associated with bacterial density, showed that the passage thorough the gut of the crabs can enrich the raw mangrove organic matter. Similar figures were obtained by Nordhaus and Wolff (2007) studying the feeding ecology of the Ocypodid *U. cordatus* in Brasil. They found that *U. cordatus* produces finely fragmented faecal material enriched in C, N and bacterial biomass compared to the sediment, concluding that the decomposition of mangrove leaf litter was greatly enhanced due to litter ingestion by this crab.

By transporting and processing a large amount of leaf litter and by acting as shredders, mangrove crabs thus propel a rapid enrichment of the primary production of mangroves (Lee, 1997).

3.4. Reduced competition among saplings by propagule predation

Propagule recruitment supports natural regeneration of mangrove forests and contributes to the restocking of vegetated stands, determining in the long term the structure and functioning of mangrove ecosystems. Thus, seed, seedling and propagule predation, mainly exerted by crabs, has been considered an important factor determining seedling distribution patterns in many mangrove stands as well as in terrestrial coastal forests (Green et al., 1997; Sherman, 2002; Lindquist and Carroll, 2004).

About mangrove forests, at least three models have been proposed to quantify and explain the impact of crab propagule predation on vegetation structure. The dominance–predation model suggests an inverse relationship between the rate of predation of a certain species and its dominance in the forest canopy (Smith, 1987), while the canopy-gap mediated model (Osborne and Smith, 1990; Clarke and Kerrigan, 2002) hypothesizes that predation could be more intense under closed canopies than in adjacent relatively large gaps. A third model, the so called flooding regime model (Osborne and Smith, 1990; Clarke and Myerscough, 1993) considers the time available for semi-terrestrial crabs to forage due to differential exposure to air of low intertidal and upper intertidal belts, suggesting that propagule predation may be related to inundation time, i.e. predation is lower in the lower intertidal.

The dominance–predation model was tested along the Australian north coast (McGuinness, 1997; Clarke and Kerrigan, 2002), in Malaysia (Smith et al., 1989), in Kenya (Dahdouh-Guebas et al., 1997,1998), in Belize (McKee, 1995), in Florida (Smith et al., 1989), in Panama (Smith et al., 1989; Sousa and Mitchell, 1999) and in the Federated States of Micronesia (Allen et al., 2003). Results of some of these studies were compatible with the model (Smith et al., 1989), whereas many studies offered alternative explanations (for example McKee, 1995; McGuinness, 1997; Dahdouh-Guebas et al., 1998; Sousa and Mitchell, 1999; Clarke and Kerrigan, 2002).

The canopy-gap mediated model postulates a more intense propagule removal in more vegetated areas, leading to negative impacts on forest regeneration and a regulating effect, exerted by reduced competition in high density stands. Recent findings that already established propagules and saplings are fed upon less than stranded ones (Dahdouh-Guebas et al., 1997; Clarke and Kerrigan, 2002) suggest that crabs can clear high density stands and thus ‘‘help’’ the already established saplings to grow better. Following this frame of hypotheses, Bosire et al. (2005) suggested a possible ‘mutual relationship’ between sesarmid crabs and mangroves, in which mangroves provide food and a suitable habitat for the crabs, which, among other roles, reduce competition through propagule predation.

The flooding regime model was challenged as well, when Sousa and Mitchell (1999) found predation to be more intense in the lower intertidal of their study area, and showed that this differential pressure was due to a greater abundance of herbivorous crabs there than in the upper intertidal, which was dominated by *Uca* spp. The temporal relationship between lagoon water level and predation intensity on specific locations has also been established experimentally by Dahdouh-Guebas (2001) and a similar model has been proposed (Fig. 2). Dahdouh-Guebas (2001) proposed a spatio-temporal biocomplexity hypothesis that explains the role of propagule predators in the shaping of vegetation structure, and how local hydrography and anthropogenic effects may influence the apparently natural process of propagule predation. Rather than the influence of many biotic and abiotic factors on a given location, it seemed to be a chain of events (i.e. spatio-temporally separated influences of one or more biotic and abiotic factors) that leads to a particular mangrove vegetation structure or zonation (Fig. 2).

3.5. Bioturbation and consequent ecosystem engineering

Although the substantial impact of crabs bioturbating activities was well known for other coastal habitats (see for example Montague, 1980; Bertness, 1985), Smith et al. (1991) were the first to use manipulative experiments to demonstrate that sesarmid crabs are crucial mangrove ecosystem engineers. Crab bioturbation significantly decreased ammonium and sulphide concentrations in mangrove soil, thus positively benefiting mangrove productivity. Recently, other studies have also examined the role of crabs in mangrove sediment biogeochemistry. Nielsen et al. (2003a,b) observed that burrows of fiddler crabs, genus *Uca*, and roots of *Rhizophora apiculata* BL. cause iron reduction to occur down to 7 cm depth.

These findings were confirmed by Kristensen and Alongi (2006) with mesocosm experiments. These authors proved that the activities of *Uca vocans vocans* (L.) affected redox sensitive elements, such as Fe and S, down to a depth of 2 cm, even if the feeding activity of these fiddler crabs was confined to the upper few millimetres of the sediment. Kristensen and Alongi (2006) hypothesised that higher content of oxidized compound forms in the upper 2 cm was caused by continuous mixing and oxidation of surface sediment due to the activity of the crabs. Interestingly, the authors suggest that mixing can occur not only during feeding but also during other activities involving movement, such as walking when the legs sink into the sediment. Also the deposition of feeding pellets and burrowing and burrow maintenance activities probably augments the effective mixing depth, resulting in a higher growth, in terms of leaves and pneumatophores, of *Avicennia marina* saplings associated with fiddler crabs (Kristensen and Alongi, 2006; Kristensen, 2008).

Crab burrows also play an important role in affecting the groundwater flow in, and the chemistry of, otherwise compact mangrove sediments (Wolanski et al., 1992), providing an efficient mechanism for exchanging water between the swamp soil and the overlying water (Ridd, 1996), and thus resulting, among other benefits, in the removal of accumulated salt from around mangrove roots (Stieglitz et al., 2000). Increased pore water exchange, caused by crabs digging activity, may result in faster removal of phytotoxins (Howes and Goehringer, 1994).

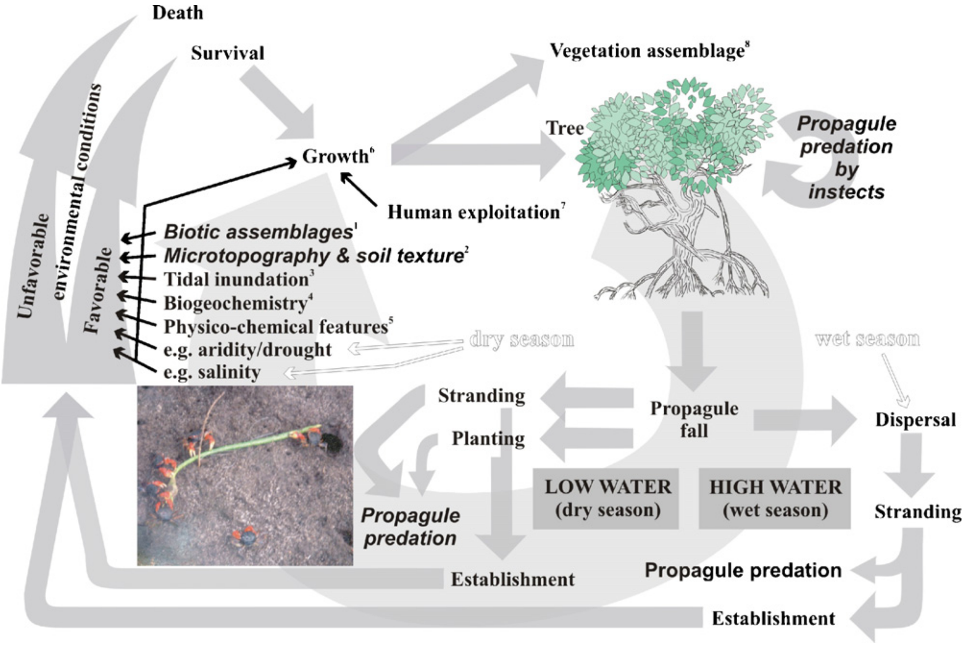

Fig. 2. The spatio-temporal biocomplexity model (Dahdouh-Guebas, 2001) indicates that when the water level is low (or during dry seasons in mangrove forests with little tidal influence) propagules fall on the soil and may plant themselves or strand (planting and stranding strategy of Van Speybroeck, 1992), the latter of which are known to be predated more than the former (Dahdouh-Guebas et al., 1997). However, the microtopographical conditions in some forests provide more possibilities to strand, increasing the exposure of propagules to predators, which in turn are very mobile and forage considerably at low water levels (Dahdouh-Guebas, 2001). When the water level is high (or during wet seasons in mangrove forests with little tidal influence), the forest is often permanently flooded for a period, and the propagules that fall under those conditions drift away through the water. They are much less likely to be affected by propagule predators, which at that time are stuck on the mangrove roots (Dahdouh-Guebas, 2001). Once the water table decreases again and propagules can establish, propagule predators further control this establishment (establishment driver). However, considering that mature propagules are less affected by propagule predators than freshly gathered ones (Dahdouh-Guebas et al., 1997), and considering that a mature stage can be reached during the dispersal period, the propagule predation that occurs when the water table decreases is likely to be less intensive. Following establishment of a propagule, various environmental conditions (filled black arrows = proximate causes) drive survival or death of the propagule (see superscript legend below). Some of these environmental drivers are most pronounced, stressing and determining for the propagule's survival during the dry season (open white arrows = ultimate causes). It seems that the forest patch structure may be the result of the differences in environmental drivers such as salinity during the dry season (development driver), but that the dispersion of propagules to lead to any vegetation structure or zonation in the first place, is controlled by the wet season (dispersion driver). Therefore, rather than the influence of many biotic and abiotic factors on a given location, it seems to be a chain of events (i.e. spatio-temporally separated influences of one or more biotic and abiotic factors) that leads to a particular mangrove vegetation structure or zonation. Superscripts indicate the following papers from the Aquatic Botany Special Issue on Mangrove Ecology dealing with these topics: (1) Nagelkerken et al. (2008), (2) Di Nitto et al. (in press), (3) Gilman et al. (2008), (4) Kristensen et al. (2008), (5) Krauss et al. (2008), (6) Komiyama et al. (2008), (7) Walters et al. (2008) and (8) Berger et al. (2008). Dark grey arrows indicate the logical sequence of events, whereas black and white arrows indicate causes or influences from. Influences exerted entirely or in part by fauna are typed in italic Arial font; the others are abiotic. The light grey arrow roughly indicates the flow of the cycle. The inset photograph shows six individuals of *Neosarmatium meinerti* struggling to conquer a *Rhizophora mucronata* propagule.

4. Molluscs and other marine taxa

4.1. Gastropods

Together with decapod crustaceans, molluscs are the most well represented taxon of marine origin in mangrove forests (Plaziat, 1984; Kathiresan and Bingham, 2001). The high mangrove mollusc diversity is probably determined by the availability of a diverse range of microhabitats (see Plaziat, 1984). In mangroves, molluscs occupy all the levels of the food web, as predators, herbivores, detritivores and filter feeders. They are zoned both horizontally (i.e. along the sea-land axis) and vertically (i.e. at diverse heights from the ground) and include both mobile and sessile species. Despite this, the overall ecological role of molluscs' and the effects they exert within the mangrove ecosystem is far from clear.

In the Indo-Pacific mangals, adults of *Terebralia palustris* Herbst (Gastropoda; Potamidae) are the only herbivorous molluscs, and for both their large size (they can reach a shell length of 16 cm, Houbrick, 1991) and their remarkable densities (among the most impressive values, Plaziat, 1984, reported 150 adults m^{-2} in New Caledonia), they are protagonists in fallen leaf consumption and degradation (Slim et al., 1997; Fratini et al., 2004). These mud whelks consume significant amounts of fallen leaves: Fratini et al. (2004) demonstrated that in a Kenyan mangrove during a single low tide, if fed ad libitum, the mud whelk population alone was able to consume about five times the daily *R. mucronata* leaf production. Moreover, *T. palustris* leaf consumption is not restricted to low tide, since this species eats at high tides too (Fratini et al., 2004) chemically locating the fallen leaves underwater. For this reason, snails are able to entrap additional primary production before it is removed by ebbing currents.

T. palustris also consumes propagules of *A. marina* and Rhizophoracea, and thus it influences mangrove restoration and regeneration (Plaziat, 1984; Dahdouh-Guebas et al., 1998;

Dahdouh-Guebas, 2001; Fratini et al., 2004; Bosire et al., 2008). The damage occurs due to the radula of adult mud whelks, and in Sri Lanka at least, it was observed that this gastropod prefers consuming the epicotyl of mangrove propagules, as opposed to crabs which feed on the hypocotyls (Dahdouh-Guebas, 2001).

Another important effect exerted by large mobile gastropods is the destabilization of the sediment due to the tracks left by their heavy shells. Carlen and Ólafsson (2002) experimentally demonstrated that the presence of adult individuals of *T. palustris* induces mud surface rearrangement, affecting the abundance of meiofauna community (decreasing density) and of the cyanobacteria carpet (complete disappearence). Overall, this induces a general modification of the biological, chemical and physical parameters of the mangrove soil surface (Carlen and Ólafsson, 2002).

4.2. Fouling communities on roots and trunks: sponges, oysters and barnacles

Mangrove roots and trunks represent zones of hard substrate colonised by fouling organisms, the dominant group of which is represented by the massive sponges (Porifera) that exert direct and indirect effects on mangrove plants. First, they increase plant growth by inducing the formation of adventitious rootlets that are able to absorb ammonium and other nitrogenous compounds produced by the sponges themselves and to transfer this ammonium into cable roots (Ellison et al., 1996). It has been demonstrated that this mechanism may increase mangrove nitrogen uptake by about 10% (Ellison et al., 1996), significant where it is often limiting. Second, due to their physical structure, sponges (as well as ascidians) protect mangrove roots from attack by wood boring isopods (Ellison and Farnsworth, 1990). By removing sponges from mangrove roots Ellison and Farnsworth (1990) estimated a 55% decrease in root growth due to isopod burrowing activity. Finally, the relation between mangroves and root-fouling sponges appears a facultative mutualism since mangrove roots are the only hard substrata available for these epibiontic organisms and they passively leak carbon to sponges tissues (Ellison et al., 1996).

Oysters and barnacles also foul mangrove roots and trunks (Pinto and Wignarajah, 1980; Ross and Underwood, 1997). The epibenthic fauna includes primary and secondary consumers, and its impact on mangrove trees is considerable: barnacle assemblage can negatively affect root growth (Perry, 1988) and heavy oyster cover can damage or break prop roots (Ellison and Farnsworth, 2001). In many mangrove forests world-wide, oysters are consumed by local people, and the breakage of the aerial roots where this mollusc grows is a consequence of oyster harvests (Pinto and Wignarajah, 1980).

4.3. Isopods

The cosmopolitan wood boring isopod *Sphaeroma terebrans* Bate (Isopoda; Sphaeromatidae) bores into the aerial roots of the fringing zone. The impact of isopod burrowing has not been definitively clarified. As a result of isopod injuries, on one hand, some documented a negative impact, due to reduction in root growth (Rehm and Humm, 1973; Perry, 1988; Ellison and Farnsworth, 1990,1992) or to the energetic costs of repairing damage (Brooks and Bell, 2002). On the other hand, Simberloff et al. (1978) demonstrated a positive effect, showing that isopod boring enhances mangrove prop root production. In East-Africa, this organism has been shown to shape mangrove tree distribution (Svavarsson et al., 2002). It therefore seems that isopods, as decapods and gastropods, are active ecological engineers in mangroves.

5. Vertebrates

From the point of view of influence on tree development and regeneration of mangroves, vertebrates are probably the least documented. A variety of fish, reptiles, birds and mammals have been observed in mangroves (Field, 1995; Stafford-Deitsch, 1996; Mastaller, 1997), but few in-depth studies exist on them. Hippopotami frequent the mangals of South Africa, and crocodiles occur in many mangrove areas throughout Australasia, Africa and Latin America (loc. cit.). Proboscis monkeys eat mangrove leaves in Borneo (Meijaard and Nijman, 2000; Verhaegen et al., 2002), deer forage on shoots in the mangals of the Sundarbans and the Florida Keys (Siddiqi and Husain, 1994; Siddiqi, 1995; Lopez et al., 2004; Barrett and Stiling, 2006) and some primates consume oysters present on mangrove roots inducing their mechanical damage or breakage (Fernandes, 1991). In Australia, sea turtles have been reported to feed on fruiting *Avicennia* propagules hanging close to the water surface (Duke, 2006). In India, one of the few studies investigating the interaction between large mammals and mangrove plants reported compensatory regrowth in *Avicennia* resulting from browsing by feral water buffaloes (Dahdouh-Guebas et al., 2006; Rist and Dahdouh-Guebas, 2006). Vegetation trampling is probably an effect from domestic cattle, but experimental studies investigating this in-depth are missing (loc. cit.). Birds and bats are known to pollinate mangrove representatives of the genus *Sonneratia* (Tomlinson, 1986; Coupland et al., 2006), while the hummingbird *Amazilia tzacatl* De la Llave is the sole pollinator of *Pelliciera rhizophorae* Triana and Planch in Central America (Prahl, 1987). Onuf et al. (1977) demonstrated that birds nesting in mangrove stands are a significant source of inorganic nitrogen for *Rhizophora* trees.

6. Conclusions

Recent acquisitions, missing pieces and open questions in the mangrove ecology puzzle.

6.1. Recent acquisitions: the impact of ocypodid crabs and gastropods

As pointed out in a number of reviews on mangrove crabs (Jones, 1984; Lee, 1998; Kathiresan and Bingham, 2001), the understanding of the strong impact of Indo-Pacific sesarmid crabs represented a real paradigm shift in mangrove ecology.

Their most ascertained ecological roles include, amongst others, retention of forest products, processing of organic matter, determination of mangrove community structure by means of differential consumption of propagules, changes in particle size distribution coupled with enhanced soil aeration (Jones, 1984; Lee, 1998).

Although Sesarmidae are still considered one of the most important taxa in shaping mangrove structure and functioning, recent literature emphasizes that other marine invertebrates can have tremendous impacts on mangrove systems. The Ocypodidae of the genus *Ucides* have a heavy impact in terms of retention of forest products and processing of organic matter on New world mangroves (Twilley et al., 1997; Nordhaus et al., 2006). Ocypodid crabs have been shown to not only have the same role of Sesarmidae, where these latter crabs are less abundant, but also to have a similar degree of impact, consuming up to 81% of the total litter production (Nordhaus et al., 2006). Moreover, other Ocypodidae, the fiddler crabs (genus *Uca*), abundant in both New and Old world mangroves, process large amounts of primary production in terms of microalgae, contributing consistently in retention of mangrove production (Jones, 1984). These small, but very abundant crabs are now considered ecosystem engineers, able to change the particle size distribution and to enhance soil aeration and mangrove primary production (Nielsen et al., 2003a,b; Kristensen and Alongi, 2006; Kristensen, 2008).

6.2. Missing pieces: ant–plant interactions

Given that ants are among the most abundant insects in mangrove ecosystems, ant–plant interactions may form an important contribution to our understanding of insect–plant dynamics in these habitats. Little attention has been devoted to mangrove ant ecology but the few studies that have addressed ant–plant interactions almost unequivocally support the idea that ants are able to provide some degree of protection against herbivore communities and the damage they inflict, including relieving mangroves from important herbivore groups such as scale insects (Diaspididae; Ozaki et al., 2000), lepidopteran larvae (Pyralidae and Geometridae; Offenberg et al., 2005), leaf beetles (Chrysomelidae; Offenberg et al., 2004a,b; Offenberg et al., 2005) and even from sesarmid male crab grazing via an indirect interaction (Offenberg et al., 2006a). Furthermore, in terrestrial agroecosystems, identical ant species are known to protect a range of crops against more than 40 different herbivores (Way and Khoo, 1992; Peng and Christian, 2004) and a multitude of empirical studies on ant–plant interactions in natural habitats support the wide distribution of ant–plant protection mutualisms (Bronstein, 1998). Hence, in terrestrial habitats ants are able to increase plant fitness. In mangrove forests there is at present, no evidence that protection against herbivore damage translates into increased plant performance affecting forest structure. This could be the focus of future mangrove ant–plant studies. It seems unlikely that ants should not have any positive effects on mangrove performance.

6.3. Open question: is herbivory by insects and crabs a positive or a negative impact?

While herbivory is usually considered to be a negative impact, this view is not straight forward and its dominance in the literature may reflect that negative impacts are more readily apparent and more readily measured than potentially positive feedbacks and energy transfers.

While the effect of insect herbivore activities may negatively impact upon certain aspects of an individual tree performance and vigour, the effect may be positive on overall ecosystem performance, for example where the loss of leaf material from a tree returns nutrients to the ecosystem, rather than having them locked up within the trees. Burrows (2003) and Feller (2002) showed that the feeding activities of leaf-feeding and wood-boring insect herbivores, respectively, altered the quality and quantity of mangrove litterfall by premature loss of younger leaves that have a higher nutrient content. The significant light gaps created by branch death resulting from the feeding activities of wood-borers (Feller, 2002) may also provide opportunities for seedling colonisation and alteration to forest structure. In essence, the true ecological role played by insect herbivores is not just confined to mere assessments of the amount of tissue lost or damaged but has its effects at the scale of whole plant performance and ecosystem functioning. Future studies of mangrove herbivory will need to be cognisant of examining the true role of insects in the ecosystem, rather than just extrapolating judgements from assessments of the amount of plant material consumed.

The same conclusions can be drafted about crab herbivory and, in particular, about their feeding on propagules. Although the negative impact of propagule removal on newly replanted stands has been identified as one of the major causes of unsuccessful reafforestation attempts, nevertheless, it remains clear that crabs can also positively influence natural mangrove regeneration (see also Steele et al., 1999; Clarke and Kerrigan, 2002; Bosire et al., 2005). Saturation of predators by shedding hundreds of propagules at once (Dahdouh-Guebas et al., 1997), or changes in palatability over time (loc. cit), which can be linked to dispersal period (Fig. 2), were suggested as possible adaptations by mangroves to propagule predation, but in-depth experimental research is lacking.

Further research in the direction of propagule removal in closed canopies/high density reforested plantations and rehabilitated stands may provide evidence of a positive impact on sapling competition for space and useful ecological information critical in the management of mangrove stands. This further research should include assessment of the indirect influence of propagule removal on other potential regeneration constraints and, ultimately, on the vegetation dynamics in reforested plantations.

At present, our conclusions are that recent work on mangrove macrobenthic impacts put new actors on the stage, for instance ocypodid crabs, ants and gastropods, revealing that the well known effects of propagule predation by sesarmid crabs and herbivory by insects are only parts of the complex faunal impact on mangrove systems. We should emphasize that, although invertebrates have strong impacts on mangrove trees, their biodiversity has a prominent role in controlling key aspects of mangrove systems, such as their biogeochemical and ecological functions (cf. Bouillon et al., 2008) and, eventually on the whole ecosystem functioning (sensu Field et al., 1998). Hence, both ecological studies and management of mangroves should be done with benthic biodiversity in mind (Duke et al., 2007; Ellison, 2008).

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References

Adams, E.S., 1994. Territory defense by the ant *Azteca trigona*: maintenance of an arboreal ant mosaic. Oecologia 97, 202–208.

Aide, T.M., 1993. Patterns of leaf development and herbivory in a tropical understorey community. Ecology 74, 455–456.

Allen, J.A., Krauss, K.W., Hauff, R.D., 2003. Factors limiting the intertidal distribution of the mangrove species *Xylocarpus granatum*. Oecologia 35, 110–121.

Anderson, C., Lee, S.Y., 1995. Defoliation of the mangrove *Avicennia marina* in Hong Kong: cause and consequences. Biotropica 27, 218–226.

Barrett, M.A., Stiling, P., 2006. Effects of key deer herbivory on forest communities in the lower Florida Keys. Biol. Conserv. 129, 100–108.

Beattie, A.J., 1985. The Evolutionary Ecology of Ant–Plant Mutualisms. Cambridge University Press, Cambridge.

Beever, J.W., Simberloff, D., King, L.L., 1979. Herbivory and predation by the mangrove tree crab *Aratus pisonii*. Oecologia 43, 317–328.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Bertness, M.D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology 66, 1042–1055.

Bosire, J.O., Kairo, J.G., Kazungu, J., Koedam, N., Dahdouh-Guebas, F., 2005. Predation on propagules regulates regeneration in a high-density reforested mangrove plantation. Mar. Ecol. Progr. Ser. 299, 149–155.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Bouillon, S., Raman, A.V., Dauby, P., Dehairs, F., 2002a. Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). Estuar. Coast. Shelf Sci. 54, 901–913.

Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002b. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130, 441–448.

Bouillon, S., Connolly, R.M., Lee, S.Y., 2008. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res. 59, 44–58.

Bronstein, J.L., 1998. The contribution of ant–plant protection studies to our understanding of mutualism. Biotropica 30, 150–161.

Brook, B.M., 2001. The effect of *Coccotrypes fallax* (Coleoptera: Scolytidae) on the recruitment of *Rhizophora stylosa* (Family Rhizophoraceae) in North Queensland Mangroves. Ph.D. Thesis, James Cook University.

Brooks, R.A., Bell, S.S., 2002. Mangrove response to attack by a root boring isopod: root repair versus architectural modification. Mar. Ecol. Progr. Ser. 231, 85–90.

Buckley, R.C., 1987. Interactions involving plants, homopterans and ants. Annu. Rev. Ecol. Systemat. 18, 111–135.

Burrows, D.W., 2003. The role of insect leaf herbivory on the mangroves *Avicennia marina* and *Rhizophora stylosa*. Ph.D. thesis, James Cook University.

Cannicci, S., Ritossa, S., Ruwa, R.K., Vannini, M., 1996a. Tree-fidelity and hole-fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). J. Exp. Mar. Biol. Ecol. 196, 299–311.

Cannicci, S., Ruwa, R.K., Ritossa, S., Vannini, M., 1996b. Branch-fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). BJ. Zool., Lond. 238, 795–801.

Carlen, A., Ólafsson, E., 2002. The effects of the gastropod *Terebralia palustris* on infanual communities in a tropical tidal mud-flat in East Africa. Wetlands Ecol. Manage. 10, 302–311.

Clarke, P.J., 1992. Predispersal mortality and fecundity in the grey mangrove (*Avicennia marina*) in southeasternAustralia. Aust. J. Ecol. 17, 161–168.

Clarke, P.J., Kerrigan, R.A., 2002. The effects of seed predators on the recruitment of mangroves. J. Ecol. 90, 728–736.

Clarke, P.J., Myerscough, P.J., 1993. The intertidal limits of *Avicennia marina* in southeastern Australia; the effects of physical conditions, interspecific competition and predation on establishment and survival. Aust. J. Ecol. 18, 307–315.

Clay, R.E., Andersen, A.N., 1996. Ant fauna of a mangrove community in the Australian seasonal tropics, with particular reference to zonation. Aust. J. Zool. 44, 521–533.

Cogni, R., Freitas, A.V.L., 2002. The ant assemblage visiting extrafloral nectaries of *Hibiscus pernambucensis* (Malvaceae) in a Mangrove forest in Southeast Brazil (Hymenoptera: Formicidae). Sociobiology 40, 373–383.

Cogni, R., Freitas, A.V.L., Oliveira, P.S., 2003. Interhabitat differences in ant activity on plant foliage: ants at extrafloral nectaries of *Hibiscus pernambucensis* in sandy and mangrove forests. Entomol. Exp. Appl. 107, 125–131.

Cole, B.J., 1980. Repetoire convergence in two mangrove ants, Zacryptocerus varians and Camponotus (Colobobsis) sp. Insect. Soc. 27, 265–275.

Cole, B.J., 1983a. Assembly of mangrove ant communities: colonization abilities. J. Anim. Ecol. 52, 349–355.

Cole, B.J., 1983b. Assembly of mangrove ant communities. Patterns of geographical distribution. J. Anim. Ecol. 52, 339–347.

Coupland, G.T., Paling, E.I., McGuinness, K.A., 2006. Floral abortion and pollination in four species of tropical mangroves from northern Australia. Aquat. Bot. 84, 151–157.

Crawley, M.J., 1989. Insect herbivores and plant population dynamics. Annu. Rev. Entomol. 34, 531–564.

Dahdouh-Guebas, F., 2001. Mangrove vegetation structure dynamics and regeneration. Ph.D. thesis, Vrije Universiteit Brussel.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Koedam, N., 1997. Food preferences in *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347, 83–89.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Van Speybroeck, D., Koedam, N., 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshwater Res. 49, 345–350.

Dahdouh-Guebas, F., Vrancken, D., Ravishankar, T., Koedam, N., 2006. Short-term mangrove browsing by feral water buffaloes: conflict between natural resources, wildlife and subsistence interests? Environ. Conserv. 34, 157–163.

Dejean, A., Dorou, S., Olmsted, I., Snelling, R.R., Orivel, J., 2003. Nest site selection by ants in a flooded Mexican mangrove, with special reference to the epiphytic orchid *Myrmecophila christinae*. J. Trop. Ecol. 19, 325–331.

Di Nitto, D., Dahdouh-Guebas, F., Kairo, J.G., Decleir, H., Koedam, N. Sea level rise effects on mangrove propagule establishment: experimental study using digital terrain modeling. Mar. Ecol. Prog. Ser., in press.

Dorou, S., Dejean, A., Olmsted, I., Snelling, R.R., 2002. Ant diversity in coastal zones of Quintana Roo, Mexico, with special reference to army ants. Sociobiology 40, 385–402.

Duke, N.C., 2002. Sustained high levels of foliar herbivory of the mangrove *Rhizophora stylosa* by a moth larva *Doratifera stenosa* (Limacodidae) in north-eastern Australia. Wetlands Ecol. Manage. 10, 403–419.

Duke, N.C., 2006. Australia's Mangroves. University of Queensland, Brisbane.

Duke, N.C., Meynecke, J.-O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Ellison, A.M., Farnsworth, E.J., 1990. The ecology of Belizean mangrove-root fouling communities: I Epibenthic fauna are barriers to isopod attack of red mangrove roots. J. Exp. Mar. Biol. Ecol. 142, 91–104.

Ellison, A.M., Farnsworth, E.J., 1992. The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. Hydrobiologia 247, 87–98.

Ellison, A.M., Farnsworth, E.J., 2001. Mangrove communities. In: Bertness, M.D., Gaines, S., Hay, M.E. (Eds.), Marine Community Ecology. Sinauer Press, Sunderland, pp. 423–442.

Ellison, A.M., Farnsworth, E.J., Twilley, R.R., 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77, 2431–2444.

Ellison, A.M., 2008. Managing mangroves with benthic biodiversity in mind: Moving beyond roving banditry. J. Sea. Res. 59, 2–15.

Elster, C., Perdomo, L., Polania, J., Schnetter, M.-L., 1999. Control of *Avicennia germinans* recruitment and survival by *Junonia evarete* larvae in a disturbed mangrove forest in Colombia. J. Trop. Ecol. 15, 791–805.

Emmerson, W.D., McGwynne, L.E., 1992. Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. J. Exp. Mar. Biol. Ecol. 157, 41–53.

Emmerson, W., Cannicci, S., Porri, F., 2003. New records for *Parasesarma leptosoma* (Hingendorf, 1869) (Crustacea: Decapoda: Brachyura: Sesarmidae) from mangroves in Mocambique and South Africa. Afr. Zool. 38, 351–355.

Erickson, A.A., Saltiss, M., Bell, S.S., Dawes, C.J., 2003. Herbivore feeding preferences as measured by leaf damage and stomatal ingestion: A mangrove crab example. J. Exp. Mar. Biol. Ecol. 289, 123–138.

Farnsworth, E.J., Ellison, A.M., 1997. Global patterns of pre-dispersal propagule predation in mangrove forests. Biotropica 29, 318–330.

Feller, I.C., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecology 65, 477–505.

Feller, I.C., 2002. The role of herbivory by wood-boring insects in mangrove ecosystems in Belize. Oikos 97, 167–176.

Feller, I.C., Mathis, W.N., 1997. Primary herbivory by wood-boring insects along an architectural gradient of *Rhizophora mangle*. Biotropica 29, 440–451.

Feller, I.C., McKee, K.L., 1999. Light-gap creation in a Belizean red-mangrove forest by a wood-boring insect. Biotropica 31, 607–617.

Fernandes, M., 1991. Tool use and predation of oysters (*Crassostrea rhizophorae*) by the tufted Capuchin, *Cebus apella apella*, in brackish water mangrove swamp. Primates 34, 529–531.

Field, C., 1995. Journey amongst mangroves. In: International Society for Mangrove Ecosystems, Okinawa.

Field, C.B., Osborn, J.G., Hoffman, L.L., Polsenberg, J.F., Ackerley, D.D., Berry, J.A., Björkman, O., Held, A., Matson, P.A., Mooney, H.A., 1998. Mangrove biodiversity and ecosystem function. Global Ecol. Biogeogr. Letts 7, 3–14.

France, R., 1998. Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. J. Trop. Ecol. 14, 413–425.

Fratini, S., Vigiani, V., Vannini, M., Cannicci, S., 2004. *Terebralia palustris* (Gastropoda; Potamididae) in a Kenyan mangal: size structure, distribution and impact on consuming leaf litters. Mar. Biol. 114, 1173–1182.

Fratini, S., Vannini, M., Cannicci, S., Schubart, C.D., 2005. Tree-climbing mangrove crabs, a case of convergent evolution. Evol. Ecol. Res. 7, 219–233.

Gara, R.I., Sarango, A., Cannon, P.G., 1990. Defoliation of an Ecuadorian mangrove forest by the bagworm, *Oiketicus kirbyi* Guilding (Lepidopetera: Psychidae). J. Trop. For. Sci. 3, 181–186.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Green, P.T., O'Dowd, D.J., Lake, P.S., 1997. Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. Ecology 78, 2474–2486.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Springer-Verlag, Berlin.

Hootsmans, M.J.M., Vermaat, J.E., Beijer, J.A.J., 1993. Periphyton density and shading in relation to tidal depth and fiddler-crab activity in intertidal seagrass beds of the Banc-Darguin (Mauritania). Hydrobiologia 258, 73–80.

Houbrick, R.S., 1991. Systematic review and functional morphology of the mangrove snails *Terebralia* and *Telescopium* (Potamididae; Prosobranchia). Malacologia 33, 289–338.

Howes, B.L., Goehringer, D.D., 1994. Porewater drainage and dissolved organic carbon and nutrient loss through the intertidal creek banks of a New England salt marsh. Mar. Ecol. Prog. Ser. 114, 289–301.

Huhta, A.P., Hellstrom, K., Rautio, P., Tuomi, J., 2003. Grazing tolerance of *Gentianella amarella* and other monocarpic herbs: why is tolerance highest at low damage levels? Plant Ecol. 166, 49–61.

Hurley, M., 1995. Leaf growth dynamics and herbivory of stinging trees (*Dendrocnide* spp.) in Australian Tropical Rainforest. Ph.D. thesis, James Cook University.

Jackson, R.V., 1995. Insect herbivory on tropical *Alphitonia* (Rhamnaceae) species. Ph.D. thesis, James Cook University, Townsville.

Johnstone, I.M., 1985. Consumption of leaves by herbivores in mixed mangrove stands. Biotropica 13, 252–259.

Jones, D.A., 1984. Crabs of the mangal ecosystem. In: Por, D., Dor, I. (Eds.), Hydrobiology of the Mangal: the ecosystem of the Mangrove Forests. Junk, Boston, pp. 89–110.

Kaly, U.L., Jones, G.P., 1998. Mangrove restoration, a potential tool for coastal management in tropical developing countries. Ambio 27, 656–661.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangroves ecosystems. Adv. Mar. Biol. 40, 84–251.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59, 30–43.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51, 1557–1571.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Kwok, P.W., 1999. Time activity budget of *Perisesarma bidens* and *Parasesarma affinis* (Brachyura: Sesarminae) at the Mai Po Marshes mangrove, Hong Kong. In: Lee, S.Y. (Ed.), The Mangrove Ecosystem of Deep Bay and the Mai Po Marshes, Hong Kong. Hong Kong University Press, Hong Kong.

Landsberg, J., 1989. A comparison of methods for assessing defoliation, tested on eucalypt trees. Aust. J. Ecol. 14, 423–440.

Landsberg, J., Ohmart, C., 1989. Levels of insect defoliation in forests: patterns and concepts. Trends Ecol. Evol. 4, 96–100.

Lee, S.Y., 1989. The importance of Sesarminae crabs *Chiromanthes* spp. and inundation frequency on mangrove (*Kandelia candel* (L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. J. Exp. Mar. Biol. Ecol. 131, 23–43.

Lee, S.Y., 1993. Leaf choice of the sesarmine crabs, *Chiromanthes bidens* and *C. maipoensis*, in a Hong Kong mangal. In: Morton, B (Ed.), The Marine Biology of the South China Sea. Hong Kong University Press, Hong Kong, pp. 597–603.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Mar. Ecol. Progr. Ser. 159, 275–284.

Lee, S.Y., 1998. The ecological role of grapsid crabs in mangrove ecosystems: implications for conservation. Mar. Freshwater Res. 49, 335–343.

Lee, S.Y., 2008. Mangrove macrobenthos: assemblages, services, and linkages. J. Sea. Res. 59 (16), 29.

Leh, C.M.U., Sasekumar, A., 1985. The food of sesarmine crabs in Malaysian mangrove forests. Malayan Nat. J. 39, 135–145.

Lindquist, E.S., Carroll, C.R., 2004. Differential seed and seedling predation by crabs: impacts on tropical coastal forest composition. Oecologia 141, 661–671.

Lopez, R.R., Silvy, N.J., Wilkins, R.N., Frank, P.A., Peterson, M.J., Peterson, M.N., 2004. Habitat use patterns of Florida Key deer: implications of urban development. J. Wildlife Manage. 68, 900–908.

Lowman, M.D., 1984. An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? Biotropica 16, 264–268.

Macnae, W., 1968. Fauna and flora of mangrove swamps. Adv. Mar. Biol. 6, 73–270.

Mastaller, M., 1997. Mangroves: the forgotten forest between land and sea. Tropic Press Sdn Bhd, Malaysia.

McGuinness, K.A., 1997. Seed predation in a tropical mangrove forest: a test of the dominance-predation model in northern Australia. J. Trop. Ecol. 13, 293–302.

McKee, K.L., 1995. Mangrove species distribution and propagule predation in Belize: an exception to the dominance-predation hypothesis. Biotropica 27, 334–345.

McKillup, C., McKillup, R.V., 1997. An Outbreak of the Moth *Achaea serva* (Fabr.) on the Mangrove Excoecaria agallocha (L.). Pan–Pac. Entomol. 73, 184–185.

Meijaard, E., Nijman, V., 2000. Distribution and conservation of the proboscis monkey (*Nasalis larvatus*) in Kalimantan. Indonesia Biol. Conserv. 92, 15–24.

Minchinton, T.E., Dalby-Ball, M., 2001. Frugivory by insects on mangrove propagules: effects on the early life history of *Avicennia marina*. Oecologia 129, 243–252.

Montague, C.L., 1980. A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. Contrib. Mar. Sci. 23, 25–55.

Murphy, D.H., 1990. The natural history of insect herbivory on mangrove trees in and near Singapore. Raffles B. Zool. 38, 119–203.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Nielsen, M.G., 1997a. Nesting biology of the mangrove mud-nesting ant *Polyrhachis sokolova* Forel (Hymenoptera, Formicidae) in northern Australia. Insect Soc. 44, 15–21.

Nielsen, M.G., 1997b. Two specialised ant species, *Crematogaster* (*australis* Mayr group) and *Polyrhachis sokolova* Forel, in Darwin Harbour mangroves. Northern Territory Nat. 15, 1–5.

Nielsen, M.G., 2000. Distribution of the ant (Hymenoptera: Formicidae) fauna in the canopy of the mangrove tree *Sonneratia alba* J. Smith in northern Australia. Aust. J. Entomol. 39, 275–279.

Nielsen, M.G., Christian, K., Birkmose, D., 2003a. Carbon dioxide concentrations in the nests of the mud-dwelling mangrove ant *Polyrhachis sokolova* Forel (Hymenoptera: Formicidae). Aust. J. Entomol. 42, 357–362.

Nielsen, O.I., Kristensen, E., Macintosh, D.J., 2003b. Impact of fiddler crabs (*Uca* spp) on rates and pathways of benthic mineralization in deposited shrimp pond waste. J. Exp. Mar. Biol. Ecol. 289, 59–81.

Nielsen, M.G., Christian, K., Henriksen, P.G., Birkmose, D., 2006. Respiration by mangrove ants *Camponotus anderseni* during nest submersion associated with tidal inundation in Northern Australia. Physiol. Entomol. 31, 120–126.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Est. Coast. Shelf Sci. 67, 239–250.

Nordhaus, I., Wolff, M., 2007. Feeding ecology of the mangrove crab *Ucides cordatus* (Ocypodidae): food choice, food quality and assimilation efficiency. Mar. Biol. 151, 1665–1681.

Odum, W.E., 1971. Pathways of energy flow in a southern Florida estuary. Sea Grant Technical Bulletin No.7. University of Miami Sea Grant Program, Miami.

Odum, W.E., Heald, E.J., 1972. Trophic analysis of an estuarine mangrove community. Bull. Mar. Sci. 22, 671–738.

Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), Estuarine Research. Academic Press, New York, pp. 265–286.

Offenberg, J., 2004. Ant–herbivore–plant interactions in a mangrove: mechanisms behind direct and indirect effects. Ph.D. thesis. University of Aarhus.

Offenberg, J., Havanon, S., Aksornkoae, S., Macintosh, D.J., Nielsen, M.G., 2004a. Observations on the ecology of weaver ants (*Oecophylla smaragdina* Fabricius) in a Thai mangrove ecosystem and their effect on herbivory of *Rhizophora mucronata* Lam. Biotropica 36, 344–351.

Offenberg, J., Nielsen, M.G., Macintosh, D.J., Havanon, S., Aksornkoae, S., 2004b. Evidence that insect herbivores are deterred by ant pheromones. Proc. R. Soc. Lond. Ser. B 271, S433–S435.

Offenberg, J., Nielsen, M.G., Macintosh, D.J., Havanon, S., Aksornkoae, S., 2005. Lack of ant attendance may induce compensatory plant growth. Oikos 111, 170–178.

Offenberg, J., Macintosh, D.J., Nielsen, M.G., 2006a. Indirect ant-protection against crab herbivory: damage-induced susceptibility to crab grazing may lead to its reduction on ant-colonized trees. Func. Ecol. 20, 52–57.

Offenberg, J., Nielsen, M.G., Macintosh, D.J., Aksornkoae, S., Havanon, S., 2006b. Weaver ants increase premature loss of leaves used for nest construction in *Rhizophora* trees. Biotropica 38, 782–785.

Offenberg, J., 2007. The distribution of weaver ant pheromones on host trees. Insectes Sociaux 54, 248–250.

Olafsson, E., Buchmayer, S., Skov, M.W., 2002. The East African decapod crab *Neosarmatium meinerti* (de Man) sweeps mangrove floors clean of leaf litter. Ambio 31, 569–573.

Onuf, C.P., Teal, J.M., Valiela, I., 1977. Interactions of nutrients, plant growth, and herbivory in a mangrove ecosystem. Ecology 58, 514–526.

Osborne, K., Smith III, T.J., 1990. Differential predation on mangrove propagules in open and closed canopy forest habitats. Plant Ecol. 89, 1–6.

Ozaki, K., Kitamura, S., Subiandro, E., Taketani, A., 1999. Life history of *Aulacaspis marina* Takagi and Williams (Hom., Coccoidea), and its damage to mangrove seedlings. J. Appl. Entomol. 123, 281–284.

Ozaki, K., Takashima, S., Suko, O., 2000. Ant predation suppresses populations of the scale insect *Aulacaspismarina* in natural mangrove forests. Biotropica 32, 764–768.

Peng, R.K., Christian, K., 2004. The weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), an effective biological control agent of the red-banded thrips, *Selenothrips rubrocinctus* (Thysanoptera: Thripidae) in mango crops in the Northern Territory of Australia. Int. J. Pest Manage. 50, 107–114.

Perry, D.M., 1988. Effects of associated fauna on growth and productivity in the red mangrove. Ecology 69, 1064–1075.

Pinto, L., Wignarajah, S., 1980. Some ecological aspects of the edible oyster *Crassostrea cucullata* (Born) occurring in association with mangroves in Negombo lagoon, Sri Lanka. Hydrobiologia 69, 11–19.

Plaziat, J.C., 1984. Mollusk distribution in the mangal. In: Por, D., Dor, I. (Eds.), Hydrobiology of the Mangal: the Ecosystem of the Mangrove Forests. Junk, Boston, pp. 111–143.

Poovachiranon, S., Tantichodok, P., 1991. The role of sesarmid crabs in the mineralisation of leaf litter of *Rhizophora apiculata* in a mangrove, southern Thailand. Phuket Mar. Biol. Centre Res. Bull. 56, 63–74.

Prahl, H. von, 1987. Notas sobre la historia natural del mangle piñuelo *Pelliciera rhizophorae* (Theaceae) en el Pacifico colombiano. Actual. Biol. 15, 117–122.

Rabinowitz, D., 1977. Effects of mangrove borer, *Poecilips rhizophorae* on propagules of *Rhizophora harrisonii* in Panama. Fla. Entomol. 60, 129–134.

Rehm, A., Humm, H.J., 1973. *Sphaeroma terebrans*: a threat to the mangroves of southwestern Florida. Science 182, 173–174.

Ridd, P.V., 1996. Flow trough animal burrows in mangrove creeks. Est. Coast. Shelf Sci. 43, 617–625.

Rist, S., Dahdouh-Guebas, F., 2006. Ethnosciences–A step towards the integration of scientific and traditional forms of knowledge in the management of natural resources for the future. Environ. Dev. Sust. 8, 467–493.

Robertson, A.I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. J. Exp. Mar. Biol. Ecol. 102, 237–248.

Robertson, A.I., 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., Giddins, R., Smith III, T.J., 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. Oecologia 83, 213–219.

Ross, P.M., Underwood, A.J., 1997. The distribution and abundance of barnacles in a mangrove forest. Aust. J. Ecol. 22, 37–47.

Schowalter, T.D., 1986. Herbivory in forested ecosystems. Annu. Rev. Entomol. 31, 177–196.

Sherman, P.M., 2002. Effects of land crabs on seedling densities and distributions in a mainland neotropical rain forest. J. Trop. Ecol. 18, 67–89.

Siddiqi, N.A., 1995. Role of crabs in the natural regeneration of mangroves in the Sundarbans forest of Bangladesh. Aust. J. Ecol. 20, 340–343.

Siddiqi, N.A., Husain, K.Z., 1994. The impact of deer on natural regeneration in the Sundarbans mangrove forest of Bangladesh. Bangladesh J. Zool. 22, 223–234.

Simberloff, D.S., Wilson, E.O., 1969. Experimental zoogeography of islands: The colonization of empty islands. Ecology 50, 278–296.

Simberloff, D., Brown, B.J., Lowrie, S., 1978. Isopod and insect root borers may benefit Florida mangroves. Science 2001, 630–632.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low nutrient diet: why do mangrove crabs eat leaves? Oecologia 131, 1–7.

Slim, F.J., Hemminga, M.A., Ochieng, C, Jannink, N.T., Cocheret de la Moriniere, E., van der Velde, G., 1997. Leaf litter removal by the snails *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). J. Exp. Mar. Biol. Ecol. 215, 35–48.

Smith III, T.J., 1987. Seed predation in relation to tree dominance and distribution in mangrove forest. Ecology 68, 266–273.

Smith III, T.J., 1994. Forest Structure. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 101–136.

Smith III, T.J., Chan, H.T., McIvor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical tidal forests from three continents. Ecology 70, 146–151.

Smith III, T.J., Boto, K.G., Frusher, S.D., Giddins, R.L., 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Est. Coast. Shelf Sci. 33, 419–432.

Sousa, W.P., Mitchell, B.J., 1999. The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos 86, 55–66.

Sousa, W.P., Kennedy, P.G., Mitchell, B.J., 2003. Propagule size and predispersal damage by insects affect establishment and early growth of mangrove seedlings. Oecologia 135, 564–575.

Stafford-Deitsch, J., 1996. Mangrove: the Forgotten Habitat. Immel Publishing Limited, London.

Steele, O.C., Ewel, K.C., Goldstein, G., 1999. The importance of propagule predation in a forest of non-indigenous mangrove trees. Wetlands 19, 705–708.

Stieglitz, T., Ridd, P., Muller, P., 2000. Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. Hydrobiologia 421, 69–76.

Svavarsson, J., Osore, M.K.W., Ólafsson, E., 2002. Does the wood-borer *Sphaeroma terebrans* (Crustacea) shape the distribution of the mangrove *Rhizophora mucronata*? Ambio 31, 574–579.

Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neoepisesarma versicolor*) offered different food sources. Estuar. Coast. Shelf Sci. 65, 213–222.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Tong, Y.F., Lee, S.Y., Moqon, B., 2003. Effects of artificial defoliation on growth, reproduction and leaf chemistry of the mangrove *Kandelia candel*. J. Trop. Ecol. 19, 397–406.

Twilley, R.R., Pozo, M., Garcia, V.H., Rivera-Monroy, V.H., Zambrano, R., Bodero, A., 1997. Litter dynamics in riverine mangrove forests in the Guayas River estuary. Ecuador. Oecologia 111, 109–122.

Vannini, M., Ruwa, R.K., 1994. Vertical migrations in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). Mar. Biol. 118, 271–278.

Veenakumari, K., Mohanraj, P., Bandyopadhyay, A., 1997. Insect herbivores and their natural enemies in the mangals of the Andaman and Nicobar islands. J. Nat. Hist. 31, 1105–1126.

Verhaegen, M., Puech, P.-F., Munro, S., 2002. Aquarboreal ancestors? Trends Ecol. Evol. 17, 212–217.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Warner, G.F., 1967. The life-history of the mangrove tree crab, *Aratus pisonii*. J. Zool., Lond. 153, 321–335.

Way, M.J., 1963. Mutualism between ants and honeydew-producing Homoptera. Annu. Rev. Ecol. Systemat. 8, 307–344.

Way, M.J., Khoo, K.C., 1992. Role of ants in pest management. Annu. Rev. Entomol. 37, 479–503.

Werry, J., Lee, S.Y., 2005. Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. Mar. Ecol. Progr. Ser. 293, 165–176.

Wetterer, J.K., O'hara, B.C., 2002. Ants (Hymenoptera: Formicidae) of the Dry Tortugas, the outermost Florida Keys. Fla. Entomol. 85, 303–307.

Wilson, E.O., 1959. Some ecological characteristics of ants in New Guinea rain forests. Ecology 40, 437–447.

Wolanski, E., Mazda, Y., Ridd, P., 1992. Mangrove hydrodynamics. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 43–62.

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Review

Organic carbon dynamics in mangrove ecosystems: A review

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Abstract

Our current knowledge on production, composition, transport, pathways and transformations of organic carbon in tropical mangrove environments is reviewed and discussed. Organic carbon entering mangrove foodwebs is either produced autochthonously or imported by tides and/or rivers. Mangrove litter and benthic microalgae are usually the most important autochthonous carbon sources. Depending on local conditions, phytoplankton and seagrass detritus imported with tides may represent a significant supplementary carbon input. Litter handling by the fauna not only affects microbial carbon transformations, but also the amount of organic carbon available for export. Most mangrove detritus that enters the sediment is degraded by microorganisms. Aerobic respiration and anaerobic sulfate reduction are usually considered the most important microbial respiration processes, but recent evidence suggests that iron respiration may be important in mangrove sediments as well. Organic carbon that escapes microbial degradation is stored in sediments and in some mangrove ecosystems, organic-rich sediments may extend to several meters depth. Many mangrove forests also lose a significant fraction of their net primary production to coastal waters. Large differences occur between mangrove forests with respect to litter production and export. Mangrove-derived DOC is also released into the water column and can add to the total organic carbon export. Numerous compounds have been characterized from mangrove tissues, including carbohydrates, amino acids, lignin-derived phenols, tannins, fatty acids, triterpenoids and *n*-alkanes. Many of these may, together with stable isotopes, exhibit a strong source signature and are potentially useful tracers of mangrove-derived organic matter. Our knowledge on mangrove carbon dynamics has improved considerably in recent years, but there are still significant gaps and shortcomings. These are emphasized and relevant research directions are suggested.

Keywords: Mangrove forest; Carbon dynamics; Import; Export; Biogeochemistry; Burial

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1. Introduction

Mangrove forests are known to be highly productive ecosystems with the capacity to efficiently trap suspended material from the water column. Litter from trees (leaves, propagules and twigs) and subsurface root growth provide significant inputs of organic carbon to mangrove sediments (Alongi, 1998). Litterfall is likely to represent about one third of the net primary production (Alongi et al., 2005a). A range of other sources may also provide important organic carbon inputs; including allochthonous riverine or marine material (e.g., seagrasses), autochthonous production by benthic or epiphytic micro- or macroalgae, and local water column production by phytoplankton (Bouillon et al., 2004). As a consequence, mangrove environments are sites of intense carbon processing with a potentially high impact to the global carbon budget (Borges et al., 2003; Dittmar et al., 2006; Alongi, 2007).

Mangrove-derived detritus is an important food source for decomposer food webs including many macroinvertebrates, such as sesarmid crabs (Grapsidae) that are notable in their ability to consume mangrove litter (Fratini et al., 2000; Cannicci et al., 2008). The more moderate, but in many cases considerable input of local or imported algal detritus is consumed by other animal species such as fiddler crabs (Ocypodidae) and various gastropods (Bouillon et al., 2002; Kristensen and Alongi, 2006). Irrespective of the pathways of organic matter consumption and food web structure, all organic matter that is not exported by tidal action enters the sediment where it is consumed, degraded and chemically modified. The degradation of organic matter in mangrove sediments is mediated by both aerobic and anaerobic microbial processes using a variety of electron acceptors. A fraction of mangrove detritus escapes degradation and is permanently buried within the mangrove sediments or adjacent ecosystems. While some mangrove forests largely retain detritus within their sediments (i.e. as degradation or burial), others lose a major fraction of their net primary production to adjacent coastal waters mainly through tidal forcing. Because of the regular tidal flooding and draining in many mangrove forests, the material exchange with adjacent waters can be very efficient.

In this contribution, we review and evaluate the current knowledge on organic carbon dynamics in mangrove ecosystems and its impact on other ecosystems. Fig. 1 provides an overview of the major pathways and pools of carbon associated with leaf litter and algal detritus in mangrove environments. We will first discuss the relative importance of various sources to the total ecosystem organic carbon balance and describe the chemical composition of mangrove tissues at the molecular level. Subsequently, we will discuss the function of food webs, including litter grazing invertebrates and microbial decomposers with emphasis on the behavior of organic carbon in mangrove sediments during early diagenesis, and the efficiency of permanent burial as a fate of mangrove production. Finally, we emphasize the role of outwelling and dispersal of mangrove derived organic matter that escapes decomposition for carbon dynamics in adjacent environments.

2. Organic carbon inputs

2.1. Mangrove ecosystem productivity

The most widely used proxy of mangrove productivity is annual litter fall, which is known to show a latitudinal gradient, being highest close to the equator (e.g., Twilley et al., 1992). Typical global average litterfall rates are in the order of ∼38 mol C m^{-2} $year^{-1}$ (Twilley et al., 1992; Jennerjahn and Ittekkot, 2002). It must be stressed, however, that this underestimates the total net CO_2 fixation by mangroves, since it does not incorporate the wood and belowground biomass production (Middleton and McKee, 2001), nor DOC release through root exudates. Estimates indicate that belowground biomass makes up a substantial part (10–55%) of the total mangrove biomass (Twilley et al., 1992; Matsui, 1998; Alongi and Dixon, 2000). A number of recent direct measurements of photosynthesis rates indeed suggest that net primary production (NPP) is significantly higher than litter fall estimates, the latter representing only ∼30% (range: 14–41%) of the net canopy production (Alongi et al., 2005a). An alternative approach to estimate the net production is to include the (scarce) estimates of wood and root production. Twilley et al. (1992) estimated a global average wood production of 67 mol C m^{-2} $year^{-1}$, taking into account the latitudinal variation. A number of data on root production have recently become available, and from these, we calculate the (geometrical) mean ratio of root to leaf

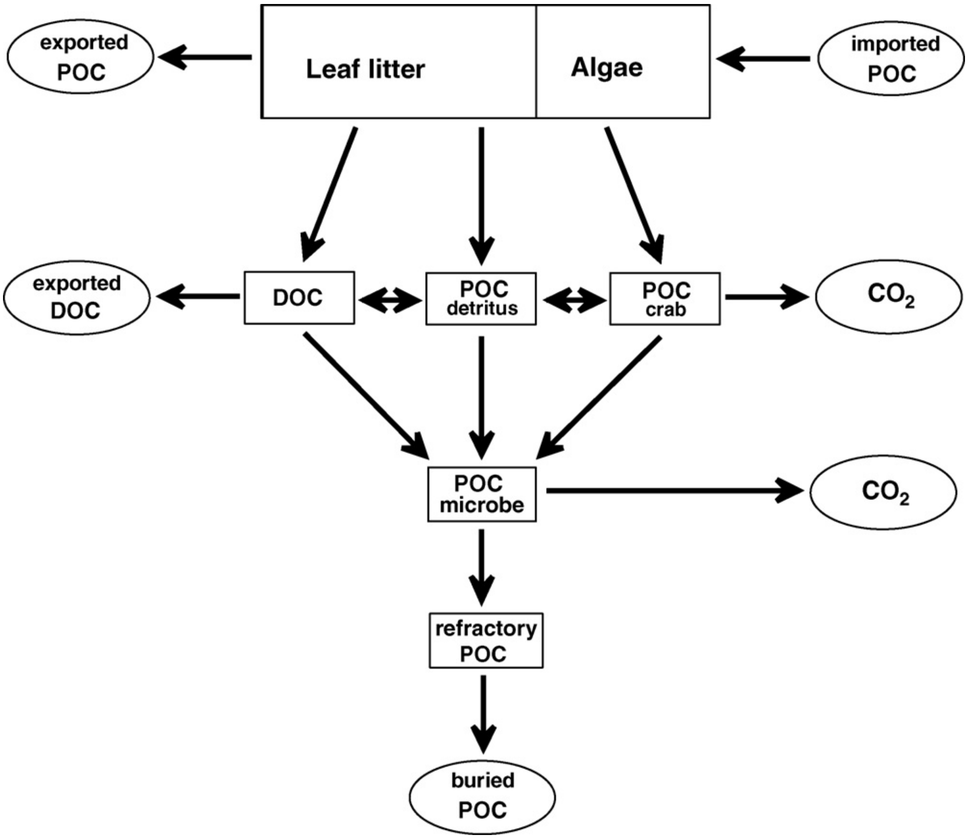

Fig. 1. Diagram showing the major pathways and pools of carbon associated with leaf litter and algal detritus in mangrove environments. Squares represent pools of organic carbon. Arrows represent transfer of carbon between pools through key processes like transport, leaching, microbial decay, and macrofaunal grazing. Ovals represent pools that are permanently displaced from biological transformation within the mangrove system (modified from Kristensen, 2008).

carbon production at 1.15 ± 0.75 ($n = 12$, data from McKee and Faulkner (2000) and Giraldo Sánchez (2005)), which allows us to estimate the global average mangrove root production at 44 mol C m^{-2} $year^{-1}$. Combining these data, the total NPP (leaf litter, wood and root production combined) can be estimated to be roughly 149 mol C m^{-2} $year^{-1}$. This suggests that litter fall comprises no more than ~25% of the total NPP, consistent with the estimates presented in Alongi et al. (2005a). So far, budgeting and productivity studies in mangrove areas have primarily been based on litterfall estimates (e.g., Jennerjahn and Ittekkot, 2002), which obviously leads to underestimates of carbon dynamics.

The efficiency of mangrove systems in trapping suspended material from the water column likely depends on a range of factors such as the particle size, salinity, tidal pumping and the areal extent of the intertidal zone (e.g., Wolanski, 1995), but can be very high: 15–44% (Victor et al., 2004), 30–60% (Kitheka et al., 2002), and up to 80% (Furukawa et al., 1997). The origin of the organic fraction in the water column is highly variable, and may include a mixture of marine or freshwater plankton, C3 or C4 terrestrial matter, mangrove litter and seagrass-derived material. The organic content of suspended matter is low, typically in the 2–4% range (Bouillon et al., 2003), which is comparable to or lower than that of mangrove sediments.

Rates of benthic primary production by microphytobenthos have been reported from different mangrove ecosystems, and range between 7 and 73 mol C m^{-2} $year^{-1}$ (Gattuso et al., 1998; Holmer et al., 2001; Kristensen and Alongi, 2006). The inputs from microalgae are generally considered to be low due to light limitation or inhibition by tannins (see Alongi, 1994). Productivity data for macroalgae are scarce, but some studies indicate that they may contribute significantly under certain conditions (e.g., 110–118 mol C $year^{-2}$ d^{-1} for lagoon systems see Koch and Madden (2001)). Phytoplankton densities and primary production have been found to be highly variable and it has been suggested that productivity may be significantly lower in estuarine mangrove areas (e.g. the Fly River delta, Papua New Guinea: 0.7–21 mol C m^{-2} $year^{-1}$, Robertson et al., 1992) than in mangrove-lined lagoons (e.g. Ivory Coast: up to 146 mol C m^{-2} $year^{-1}$, see references in Robertson and Blaber, 1992). The relative importance of phytoplankton to the total mangrove ecosystem primary productivity is expected to vary with geomorphology, water currents, turbidity and nutrient levels, e.g., ~20% for the Fly River delta, Papua New Guinea (Robertson et al., 1992), 50% in Terminos Lagoon, Mexico (Day et al., 1987), and far exceeding mangrove inputs in other ecosystems (e.g. Wafar et al., 1997; Li and Lee, 1998). Despite a potentially high phytoplankton production in mangrove creeks, high turbidity and active microbial degradation within the water maintain many creeks as net heterotrophic systems, even during the day (Kristensen and Suraswadi, 2002).

2.2. Origin of mangrove organic carbon

Elemental composition and stable isotope signatures can provide clues on the origin of the sedimentary organic matter pool. Much of the variation in these proxies can be explained by a simple two-source mixing model whereby mangrove litter (characterized by high POC, high POC/PN ratios, and low $\delta^{13}C$ values) and suspended matter (low POC, low POC/PN ratios, variable but generally higher $\delta^{13}C$ values) are taken as end-members (Bouillon et al., 2003), similar to what has been found in salt marsh ecosystems (Middelburg et al., 1997). However, due to the limited number of studies which have simultaneously reported $\delta^{13}C$ values and POC and/or POC/PN data from mangrove sediments, the data presented in Bouillon et al. (2003) hold little information on the relative occurrence of the different situations encountered. A compilation of available data (Fig. 2A) shows that 58% of $\delta^{13}C$ data are lower than −25‰, and thus suggest an important input of mangrove litter ($\delta^{13}C \sim -28$ to −30‰). On the other hand, the significant number of relatively high $\delta^{13}C$ data (−17 to −23‰) indicates large inputs of imported (phytoplankton, seagrasses in some ecosystems) and possibly local (microphytobenthos) ^{13}C-enriched ($\delta^{13}C \sim -16$ to −24‰) carbon sources. Accordingly, Wooller et al. (2003) suggested that dense microbial mats may provide a high input of organic carbon to certain mangrove sediments (up to 90%), and similarly, Marchand et al. (2003, 2005) provided clear evidence that algal material can represent a significant fraction of the sedimentary organic carbon, in particular during the early stages of mangrove forest development.

Mangrove sediments are in general relatively rich in organic carbon with a median POC content of 2.2% (Fig. 2B). A fraction of 44% of the available data show POC less than 2% and 28% with values between 2 and 5%. Since most mangrove forests occur along sedimentary coastlines in large estuaries and deltas, large quantities of suspended organic carbon brought in by tides or rivers are deposited along with local mangrove detritus (e.g. Victor et al., 2004 and references therein). The large majority (96%) of mangrove sediments have POC/PN ratios above 10 (Fig. 2C), which is typical for subtidal marine sediments, and 47% even exceed POC/PN ratios of 20. Although the large fraction of relatively high POC/PN ratios indicate that mangrove sediments contain a significant input of mangrove litter, the wide range is difficult to interpret. It may reflect either pure mangrove litter in an advanced stage of decomposition, or a variable contribution by other carbon sources. Apart from the indications outlined above, recent results based on the isotope composition of sediment organic carbon from mangrove systems where significant amounts of C4 vegetation occurs in the catchment areas, points out the potential importance of riverine-transported terrestrial material in mangrove systems (Bouillon et al., 2007a; Ralison and Bouillon, unpublished).

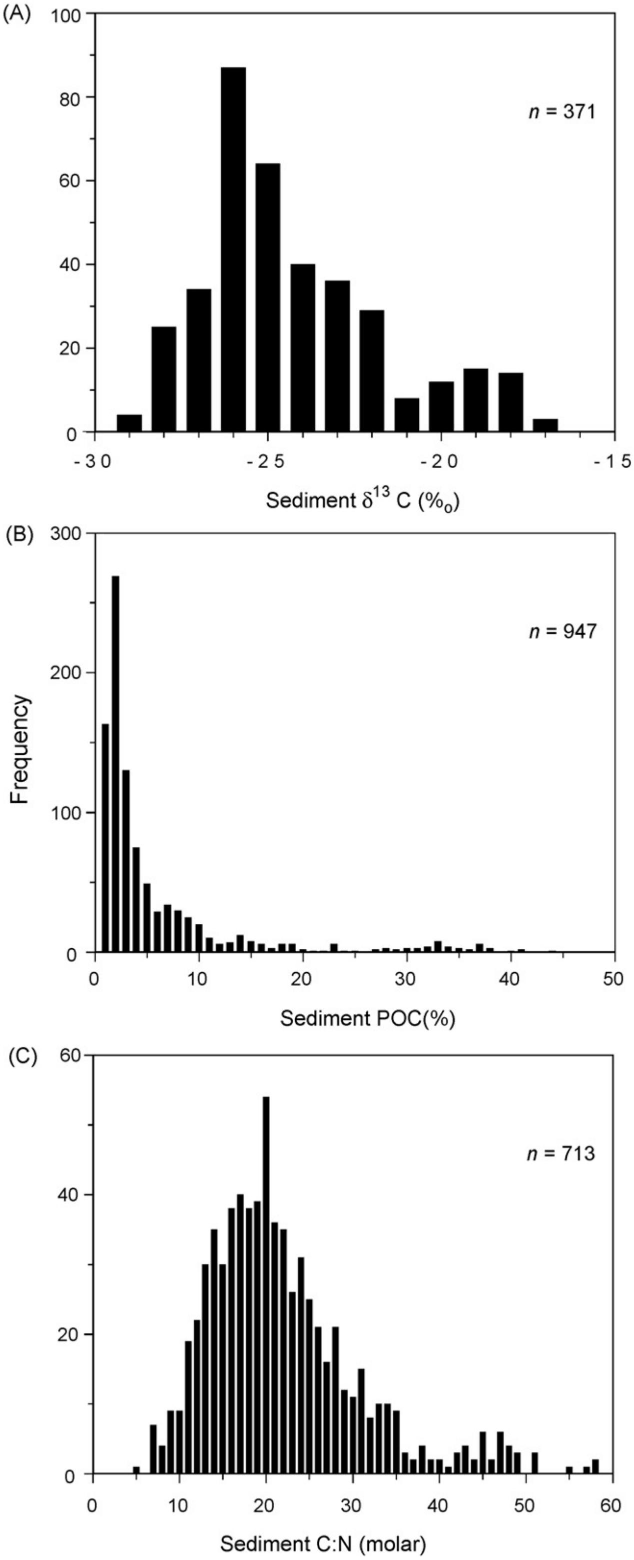

Fig. 2. Compilation of (A) bulk $\delta^{13}C$, (B) bulk POC and (C) bulk POC:TN ratios of intertidal mangrove sediments. Only data where POC and POC:TN ratios were analyzed using standard elemental analyzer approaches are included. Compiled from various sources. The data and references are available upon request.

3. Chemical composition of mangrove litter

Mangrove tissues (in particular *Rhizophora* leaves) have been characterized in various studies that focused on: (i) the nutritional quality of mangrove-derived organic matter, (ii) the specificity of certain biomarkers to trace mangroves in paleoenvironmental reconstructions, or (iii) the organic fluxes delivered to the oceans. Numerous compound classes have been identified, including carbohydrates, amino acids, lignin-derived phenols, tannins, fatty acids, triterpenoids and *n*-alkanes, and up to 50% of *Rhizophora* leaf biochemical composition can now be accounted for (Hernes et al., 2001). The general conclusion is that mangrove tissues exhibit a strong source signature and that some compounds are potentially useful tracers of mangrove-derived organic matter as they are preserved during diagenesis. These biochemical tracers can provide important complementary information for a successful interpretation of stable isotope data.

3.1. Carbohydrates

Carbohydrates represent the largest fraction of photosynthetically assimilated carbon in the biosphere. They are the most abundant constituents of vascular plants where they mostly occur in cell walls. Total carbohydrate yields can represent up to 65.5% of organic carbon in mangrove wood (Opsahl and Benner, 1999). Marchand et al. (2005) showed that the leaves of three different mangrove species (*Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle*) are poorer than woody tissues in neutral sugars, with concentrations ranging from 12 to 32% and from 25 to 36% of the total organic carbon, respectively. Glucose is the most abundant neutral sugar in each of these species, representing >50% of the total. About 80% of the glucose was found to be cellulosic, while other neutral sugars are mostly hemicellulosic. Moers et al. (1990) and Benner et al. (1990) demonstrated that *R. mangle* wood is mainly composed of glucose, xylose and arabinose, whereas the compositional pattern in *R. mangle* leaves is: glucose > arabinose > galactose > rhamnose > xylose. Leaves of *A. germinans* are richer in xylose compared with leaves from other mangrove species (Marchand et al., 2005; Opsahl and Benner, 1999). Even though mangrove tissues have typical carbohydrate signatures, these tend to disappear rapidly in the detritus pool since polysaccharides are highly reactive compounds relative to bulk organic carbon, and since microbial communities themselves synthesize new polysaccharides. Nevertheless, neutral carbohydrates show selective degradation patterns in mangrove sediments, which can provide specific details on their sources, despite their overall low concentrations. Marchand et al. (2005) showed that the debris deriving from mangrove roots strongly contributes to the organic enrichment of sediments, and can be discriminated using their content of xylose, and cellulosic monosaccharides. In contrast, algal mats developing on the sediment surface during the early stages of mangrove development are responsible for abundant rhamnose content.

3.2. Amino acids

Amino acids can represent up to 9% of mangrove leaf biomass (Hernes et al., 2001), but very few studies have described their composition in mangrove tissues. Zieman et al. (1984) reported concentrations of total amino acids in *Rhizophora* leaves of 833 μmol g^{-1} with glutamic acid, leucine, and glycine representing each more than 10%. *Avicennia* leaves, on the other hand, contain mostly glycine, glutamic acid and aspartic acid (Tremblay and Benner, 2006). The concentration of amino acids tends to increase during decomposition due to microbial accumulation (Hernes et al., 2001; Tremblay and Benner, 2006). Since amino acids of prokaryote origin then become prevalent, their use as mangrove tracers appears limited.

3.3. Tannins

Tannins in vascular plants occur as two types, condensed and hydrolysable. They are more abundant in plant leaves than in woody tissues, and contribute to the color and astringency of the bulk organic matter. Hernes et al. (2001) found that green leaves of *R. mangle* may contain more than 6% tannins, being third in abundance after polysaccharides (21%) and amino acids (9%). The tannin content of mangrove leaves is higher and more polymerized than found for 40 other dicotyledonous plant species (Hernes et al., 2001). Condensed tannin consists of 80% procyanidin and 20% prodelphinidin. The latter, with its higher degree of hydroxylation, appears to be more labile than procyanidin tannin. Leaching, which induces an increase in polymerization of condensed tannin, is an important mechanism for tannin removal from leaves. Hernes et al. (2001) concluded that while the composition of brown and partly decomposed leaves is recognizable as dicotyledonous in origin, it is difficult to attribute the composition specifically to mangrove leaves.

3.4. Lignin-derived phenols

Lignin is a nitrogen-free co-polymer of various phenylpropenyl alcohols that is present in vascular plants. Lignin composition varies significantly between gymnosperms and angiosperms, and between hard (i.e., woods) and soft (i.e., leaves, needles) tissues. Because of the exclusive association with higher plants, lignin is usually considered as a specific tracer of terrestrial plant remains. Mangrove species exhibit a typical vascular-plant lignin signature, with great variations between leaves and wood, the latter being richer in lignin oxidation product. Marchand et al. (2005) reported a total yield of eight simple phenols ranging from 0.5 to 1.5% and from 3.8 to 5.1% of TOC in leaves and wood material, respectively. Mangrove wood is characterized by very low ratios between cinnamic phenols and vanillic phenols (C/V), whereas these ratios for mangrove leaves are an order of magnitude higher than for other dicotyledonous angiosperm leaves (Dittmar and Lara, 2001b; Marchand et al., 2005). The ratio between syringic phenols and vanillic phenols (S/V), on the other hand, is higher for woody tissues than for herbaceous tissues. The acid-to-aldehyde ratios of both vanillic and syringic phenols in mangrove leaves are also unusually high compared to non-mangrove leaves, whereas in woody tissues, these ratios are close to zero (Opsahl and Benner, 1995; Dittmar and Lara, 2001b; Marchand et al., 2005). Lignin is generally thought to be more refractory than other molecular compounds, and Marchand et al. (2005) found that lignin-derived phenols were lost at a lower rate during decomposition than total neutral sugars and bulk organic carbon. Decomposition pathways changing the monomer ratios are known to be dependent of the redox conditions (Dittmar and Lara, 2001b; Marchand et al., 2005).

3.5. *Fatty acids*

Fatty acids are ubiquitous in living organisms, and due to their biological specificity can act as biomarkers for prokaryotes, fungi, diatoms, dinoflagellates or vascular plants. They are therefore useful tracers of the origin and flow of mangrove-derived organic carbon trough estuarine food webs. Recently, Meziane et al. (2007) showed that leaves of six mangrove species can be differentiated using their fatty acid profiles, and that geographically-separated populations of the same species can be identified. Saturated fatty acids (SAFA) dominate the fatty acid composition of mangrove leaves with Palmitic acid (16:0) as the most abundant (Sassen, 1977; Mfilinge et al., 2003, 2005; Hall et al., 2006). The high content of polyunsaturated fatty acids (PUFA), in particular 18:2ω6 and 18:3ω3, has been identified as useful biomarkers of mangrove leaves in estuarine food chains (Sassen, 1977; Hall et al., 2006; Meziane et al., 2007). Mangrove leaves also include the long-chain fatty acids (LCFA) 24:0, 26:0 and 28:0, which are typical vascular plant markers (Alfaro et al., 2006; Hall et al., 2006; Meziane et al., 2007). Mfilinge et al. (2003) suggested that the amount of 16:0 in mangrove leaves may be an indicator of degradation state since the concentration of SAFA in detritus declines constantly with age. Conversely, the concentrations of LCFA do not change with detritus age, suggesting that these vascular plant-markers can be useful biomarkers (Mfilinge et al., 2003, 2005).

3.6. *Triterpenoids*

Pentacyclic triterpenoids have frequently been used to characterize sources of sedimentary organic matter as they are common constituents of plants. Dodd et al. (1998) reported 11 triterpenoids in epicuticular waxes accounting for up to 3.5% of *Rhizophora mangle* leaves from West Africa. Taraxerol (taraxer-14-en-3β-ol) is not specific to *Rhizophora* but occurs in unusually high concentrations in its leaves compared to other vascular plants (Killops and Frewin, 1994; Koch et al., 2003; Versteegh et al., 2004). Taraxerol is mainly present inside the leaf, whereas β-amyrin (olean-12-en-3β-ol) is dominant in epicuticular waxes. Leaves of *Rhizophora* are also characterized by high amounts of germanicol (olean-18-en-3β-ol) and lupeol (lup-20(29)-en-3β-ol). *Avicennia germinans* mainly contains betulin (lup-20(29)-en-3β,28β-diol), lupeol and β-sitosterol (24-ethylcholest-5-en-3β-ol), whereas significant quantities of β-sitosterol and lupeol are typical of *Laguncularia racemosa* (Koch et al., 2003). Oku et al. (2003) suggested that triterpenoids may have a special function in the adaptation of mangrove to salt stress, which may explain their richness. While betulin, tracer of *Avicennia*, can be efficiently degraded in the sediments, taraxerol seems to be unreactive with respect to microbial degradation (Killops and Frewin, 1994; Hernes et al., 2001; Versteegh et al., 2004; Koch et al., 2005). Consequently, taraxerol can be a useful proxy for paleoenvironmental reconstructions.

3.7. *n-Alkanes*

Long-chain *n*-alkanes (between 25 and 35 carbons), that are characteristic components of epicuticular waxes of mangrove leaf surfaces, can also be used as tracers of higher plant remains (Dodd et al., 1995, 1998; Rafii et al., 1996; Versteegh et al., 2004). Versteegh et al. (2004) and Mead et al. (2005) found that the most abundant lipid at the *Rhizophora* leaf surface, C29 *n*-alkane, accounts for 0.22% of the dry leaf material. However, it seems that the *n*-alkanes composition in mangrove plants is susceptible to biogeographic variations. Rafii et al. (1996) and Dodd et al. (1998) reported unusually high concentration of C28 *n*-alkane in *Avicennia* and *Rhizophora* from French Guiana, whereas C31 is also important in plants of these genera in West Africa. Foliar wax from *Laguncularia racemosa* in French Guiana contains, among a broad range of *n*-alkanes, high concentrations of C29 and C33 whereas this species in West Africa mostly contains C27-C29. Dodd et al. (1999) suggested that the *n*-alkane composition of mangroves can be linked to environmental conditions, and attributed the dominance of longer chained C31 and C33 *n*-alkanes of *A. marina* in the United Arab Emirates to its evolution under arid conditions.

4. Mangrove foodwebs and the role of fauna in organic carbon processing

Mangrove forests are recognized as an important habitat for fauna, harboring often abundant and diverse benthic invertebrate communities (Sasekumar, 1974; Wells, 1984; Nagelkerken et al., 2008). These may further serve as important food sources for transient fauna (e.g., Sheaves and Molony, 2000) and a number of species are commercially important and are harvested for food consumption (Rönnbäck, 1999; Rönnbäck et al., 2003; Walters et al., 2008). The exact role of mangrove ecosystems in attracting and sustaining these communities has been long debated, but likely results from a combination of offering suitable habitat, food supply, and refuge from predators (e.g., Laegdsgaard and Johnson, 2001). While a general overview of mangrove food webs has recently been presented in a different context (Bouillon et al., 2008; Nagelkerken et al., 2008) and is outside the scope of this paper, we will here focus on the different food sources that may be used by mangrove benthos and the potential impact of fauna to the overall carbon budget and sediment biogeochemistry.

Mangrove trees have traditionally been viewed as the main supplier of organic carbon to mangrove benthos, and their production was thought to fuel not only local faunal communities, but also adjacent aquatic foodwebs through outwelling (e.g., Odum and Heald, 1975). It is now recognized that the outwelling hypothesis needs to be reconsidered or at least put into perspective (see later), and recently it has been demonstrated that the view of mangrove litter as being the dominant food source in the intertidal zone is too simplified. It has become increasingly clear that mangrove invertebrates exploit a wide range of potential food resources, including mangrove litter, epiphytic algae, benthic microalgae, bacteria and fungi, as well as macroalgae and a mixture of organic sources imported from adjacent aquatic environments by tidal currents (Bouillon et al., 2002; Hsieh et al., 2002; Kieckbusch et al., 2004). Thus, the degree of utilization of mangrove-derived food sources depends partially on the degree of material exchange with adjacent systems (Bouillon et al., 2004). Considering their overall abundance and high secondary productivity, consumers may have a profound impact on the overall organic carbon dynamics in mangrove systems. First, we can expect that the overall consumption rate of organic carbon (whatever its origin) is high and that selective feeding on certain food sources may significantly alter the relative amounts of different sources available for export, burial, or mineralization. Secondly, fauna process much higher amounts of material than they actually assimilate, and this can result in important modifications of the size, form or quality of the non-assimilated organic matter, which in turn may have implications for its availability for export, consumption, or mineralization.

4.1. Qualitative importance of fauna in organic carbon dynamics

The foraging and feeding activities of mangrove fauna can influence the properties and availability of organic carbon through a number of different mechanisms. The most well-known example is the leaf litter removal capacity of sesarmid crabs (or the ocypodid crab *Ucides cordatus* in parts of the New World). Thongtham and Kristensen (2005) showed that *Neoepisesarma versicolor* consumes fresh green and senescent yellow *Rhizophora apiculata* leaves at considerably lower rate than partly degraded brown leaves. This observation is consistent with those of Giddins et al. (1986) for *Neosarmatium smithii* and Micheli (1993) for *Sesarma messa* and *N. smithii*. The higher palatability of brown leaves compared with green and, in particular, yellow leaves probably results from improved nutritional value and removal of inhibitory compounds by the ageing process (Poovachiranon and Tantichodok, 1991). The feeding activity of sesarmid crabs not only affects the availability of leaf litter on the forest floor and its subsequent export, but many of these crabs typically take the leaves down in their burrow for storage, where they continue to decompose (Skov and Hartnoll, 2002). Moreover, the removal of leaves from the surface is likely to be beneficial for the growth of microalgae, since these are hypothesized to be inhibited by tannins (Alongi, 1994), in which mangrove leaves are particularly rich. Sesarmid crabs ingest twice as much material than they actually assimilate (Thongtham and Kristensen, 2005), which means that half of the ingested litter subsequently becomes available as faeces for decomposer or detritus food webs. This processing of leaf material may have far-reaching consequences, since the nitrogen-rich faecal pellets are more accessible for feeding by other invertebrates due to the smaller size of the particle fragments (Lee, 1997, 1998), and have significantly higher decomposition rates compared to the original material (Lee, 1997; Kristensen and Pilgaard, 2001), resulting in a much faster turnover of organic carbon.

Deposit-feeding invertebrates such as ocypodid crabs, a range of sesarmid crabs and gastropods also process large amounts of sediment and associated organic material, which is often fed upon very selectively, either at the stage of ingestion or during assimilation (e.g., Dye and Lasiak, 1987). These selective feeding activities not only result in a modification of the amount and relative quantities of different sources of organic carbon, but also modify the sediment surface properties. Exclusion experiments have shown that grazing by epifauna significantly reduces microalgal standing stocks (Branch and Branch, 1980; Webb and Eyre, 2004; Kristensen and Alongi, 2006), which in combination with the physical modifications and disturbance of the sediment surface, may have a number of indirect effects on microbial and meiofaunal communities (Dye and Lasiak, 1986; Schrijvers et al., 1998).

A final important process through which faunal communities influence organic carbon dynamics is their burrowing activity. The resulting mixing of sediment material from different depths and the increased oxygenation around burrows results in significant local changes in the relative importance of microbial decomposition pathways (Kristensen, 2008) and enhances the re-oxidation of reduced compounds (e.g. Fe^{2+} and H_2S). Furthermore, burrows of crabs and other benthic fauna have been shown to significantly increase the hydraulic conductivity of mangrove sediments (Susilo et al., 2005; Mazda and Ikeda, 2006), which enhances the porewater-mediated export of dissolved nutrients and organic carbon to the aquatic environment.

4.2. Quantitative importance of fauna on organic carbon fluxes

Activities of mangrove fauna can have a profound quantitative impact on the availability, properties, and fate of organic matter. Leaf litter removal by crabs is not only affecting the amount of organic carbon available for export, but also the potential role of litter consumption for the overall carbon budget of mangrove systems should be stressed. This can be illustrated conceptually from scenarios where the amount of leaf litter that is potentially removed, ingested and assimilated by sesarmids feeding on a pure litter diet is estimated from literature data and a number of simple assumptions (Table 1). The essential data on biomass of sesarmids, handling rate, consumption rate and assimilation efficiency are quite variable among mangrove environments. Since the biomass of sesarmids varies widely, i.e. from 150 to

Table 1
Conceptual scenarios showing the potential litter consumption by sesarmid crabs

	Scenario 1		Scenario 2		Scenario 3	
Biomass of sesarmids (g m^{-2})	150		250		400	
Consumption rate (mmol C m^{-2} d^{-1})	105		175		280	
Dependency on litter (%)	30	60	30	60	30	60
Litter consumption in % of litterfall	30	60	50	100	80	160

Scenarios with "low" (1), "medium" (2) and "high" (3) crab biomass are presented. Total carbon consumption rates of sesarmid crabs are derived from the literature (see text for references). The chosen range of crab dependency of litter in the diet is based on stable isotope data presented in Bouillon et al. (2004). The fraction of the average litterfall that is potentially consumed is estimated assuming an average litter fall rate of 105 mmol C m^{-2} d^{-1} (see text for more details).

750 g m^{-2} (Wells, 1984; Emmerson and McGwynne, 1992; Skov and Hartnoll, 2002), three different biomass values (low, medium and high) within these limits were used here in order to provide realistic scenarios. Potential consumption rates by sesarmid crabs offered food in excess are reported to range from 500 to 1000 μmol C (g ww crab)$^{-1}$ d^{-2} (Emmerson and McGwynne, 1992; Lee, 1998; Ólafsson et al., 2002; Gillikin et al., 2004; Thongtham and Kristensen, 2005), and an intermediate value of 700 μmol C (g ww crab)$^{-1}$ d^{-2} was used in our calculations. For litter fall, a global average value of ~105 mmol C m^{-2} d^{-1} was used (Jennerjahn and Ittekkot, 2002 and discussion above). The exact dependency of sesarmids on mangrove litter may vary according to the species and sites considered (see above and Cannicci et al., 2008), but two values, 30 and 60% were used to cover a realistic range (Bouillon et al., 2004). The estimated fraction of leaf litter removed is highly variable (Table 1) and even a low sesarmid biomass and a low dependency on mangrove litter result in a considerable removal (30%). When sesarmid biomass is high and their reliance on mangrove litter is also high, the average litter fall rate is insufficient to sustain sesarmids under the assumptions made. The deficit becomes even more pronounced from the fact that crabs only are capable of removing 30–90% of the litterfall (Robertson, 1986; Micheli, 1993; Slim et al., 1997; Schories et al., 2003), while the remainder is either exported or degraded by microorganisms.

Although these calculations should be considered rather an exercise than a precise estimate, they do demonstrate that a dominant role for mangrove litter in the diet of consumers is not required to explain high litter removal rates, and hence, that the overall effect of faunal consumption on litter dynamics can be very high, even when other inputs would be the main sources sustaining faunal production. Also, under the assumptions mentioned above, food limitation might occur when relatively high densities of litter consumers are present. This has also been pointed out recently for *Ucides cordatus* by Nordhaus et al. (2006). They found that leaf inputs are insufficient to support the food requirements of the resident crab populations during periods of reduced litterfall. Leaf litter is clearly a major component in the diet of most sesarmid crabs (Dahdouh-Guebas et al., 1997), and litter carbon appears sufficient to support their growth. However, the low nitrogen availability in litter forces these crabs to obtain this element from other sources. Thongtham and Kristensen (2005) hypothesized that sesarmids primarily supplement their leaf diet by occasional ingestion of nitrogen-rich animal tissues (e.g. invertebrates and fish carcasses) since other potential nitrogen sources, such as prokaryote, fungi and benthic primary producers, only provide a limited amount of the needed nitrogen. Accordingly, Dahdouh-Guebas et al. (1999) observed that only few non-ocypodid crab species from Kenyan mangrove forests are specialized plant eaters. Most of them supplement their diet with animal prey, mostly bivalves, gastropods, anomurans and other brachyurans.

Furthermore, given that the abovementioned estimates only refer to sesarmid crabs, it becomes evident that when we consider the entire community of epifauna and infauna, their impact on organic matter cycling and litter dynamics can be substantial. Data on secondary production coupled to information on resource utilization, which are entirely lacking for any mangrove system, would be required to obtain a realistic estimate of this role. The impact of fauna in current mangrove carbon budgets is often considered only in terms of direct herbivory or invoked to estimate the proportion of leaf litter retained within the system due to burial and/or consumption. Future ecosystem budgets should attempt to evaluate the potential role of resident fauna from a trophic point of view and include a wider variety of methodological approaches.

5. Organic matter decomposition and mangrove sediment biogeochemistry

5.1. *Early stages of decomposition*

Irrespective of the pathways and food web structure involved, all mangrove organic matter that is not exported by tidal action enters the sediment and is degraded or chemically modified by microorganisms. The decay of deposited mangrove litter begins with significant leaching of soluble organic substances. Newly-fallen mangrove litter loses 20–40% of the organic carbon by leaching when submerged in seawater for 10–14 days (Camilleri and Ribi, 1986; Twilley et al., 1997). The carbohydrates that rapidly leach after submersion in water are mostly the non-lignocellulose components (Neilson and Richards, 1989). Accordingly, Benner et al. (1990) observed that 97% of cyclitols are rapidly lost from decaying mangrove leaves. Also tannins and other phenolic compounds with microbial inhibitory potential account for a significant fraction (up to 18%) of the dissolved organic matter (DOM) in mangrove leachate (Benner et al., 1986). This is associated with a decrease in tannin content from 59 mg g^{-1} in senescent yellow leaves to 5.5 mg g^{-1} in partly degraded brown leaves (Hernes et al., 2001). Much of the leached DOM is actually labile and degraded efficiently under oxic and nutrient replete conditions with conversion efficiencies into microbial biomass of up to 90% (Benner et al., 1986; Kristensen and Pilgaard, 2001). In nutrient-limited and partly anoxic mangrove sediments, on the other hand, the microbial incorporation occurs with a lower average efficiency of roughly 35% (Boto et al., 1989).

Further decomposition of the remaining particulate material occurs through extracellular enzymatic hydrolysis which is mediated by aerobic and anaerobic prokaryotes and marine mycelial decomposers such as eumycotes (fungi) and oomycotes (protoctista) (Newell, 1996). These latter organisms are highly-adapted for the capture of cellulose-rich vascular plant litter by pervasion and digestion from within. Thus, the polysaccharide (i.e. cellulosic) components of lignocellulose are generally degraded about twice as fast as the lignin component, indicating that mangrove detritus becomes relatively enriched in lignin-derived carbon with time (Benner and Hodson, 1985; Marchand et al., 2005). While cellulose and lignin can readily be degraded in oxic environments, these compounds are only slowly degraded under anoxic conditions. Lignin, for example, has a half-life of more than 150 years in anoxic mangrove sediments (Dittmar and Lara, 2001b).

The chemical changes that occur in mangrove detritus during degradation are not only caused by enzymatic cleavage and gradual loss of substances. Tremblay and Benner (2006) reported that the total hydrolysable amino acid content of leaves increases up to five-fold during a 4-year decomposition phase due to accumulation of microbial biomass. This is consistent with a general decrease in C:N ratios observed during the decomposition of mangrove leaves (Twilley et al., 1986; Robertson, 1988; Thongtham and Kristensen, 2005). The fatty acid composition in mangrove leaves also changes from the predominantly plant dominated saturated fatty acids to monounsaturated fatty acids and branched chain fatty acids indicative of prokaryote biomass (Mfilinge et al., 2003, 2005).

The decomposition rate of newly-fallen litter has been examined in numerous litterbag studies. The decay typically follows a single exponential pattern ($M_t = M_0\,e^{-kt}$, M_t is the mass remaining after time t, M_0 is the initial mass and k is the decay constant). Decay constants of yellow leaves deposited on intertidal mangrove sediment varies about two orders of magnitude (e.g. 0.001–0.1 d^{-1} corresponding to a half life of 693 to 7 days) (Tam et al., 1998; Aké-Castillo et al., 2006). Although comparison among studies is complicated by methodological constraints (e.g. different mesh size in bags, pre-handling of litter and incubation time), a number of studies have shown indications of several mechanisms controlling litter degradation in mangrove environments, such as inundation frequency, abundance of detritivorous fauna, mangrove species, and the initial C:N ratio. For instance, Middleton and McKee (2001) found from own and literature data that mangrove litter placed on frequently inundated low intertidal sediments lost on average $0.64 \pm 0.11\%$ dw d^{-1}, while the decay on dry upper intertidal sediments only accounted for $0.32 \pm 0.08\%$ dw d^{-1}. The difference is obviously caused by the greater accessibility to microbial degraders when litter is permanently wet. The role of small fauna (excluding crabs) is clearly evident from the study of Bosire et al. (2005), in which the decay of *Rhizophora mucronata* and *Sonneratia alba* litter appeared strongly dependent on the total abundance of amphipods, nematodes, turbellarians, isopods and polychaetes (Fig. 3). The shredding and macerating activities of these animals apparently increase the degradability of litter material by increasing the effective surface area accessible to microbial attack. It is obvious that the action of leaf-eating sesarmid crabs will augment this faunal effect outside litterbags where their influence is also allowed (Poovachiranon and Tantichodok, 1991; Robertson et al., 1992; Kristensen and Pilgaard, 2001).

Despite the inherent variability among litterbag studies, a number of reports have independently found an inverse relationship between the C:N ratio of mangrove leaf litter and the decay constant. Even when these studies are combined, the relationship is still significant ($p < 0.01$, Fig. 4). Litter degradation seems therefore strongly dependent on the availability of nitrogen for the microbial decomposers. The difference in degradability and elemental composition appears to be a dual function of species (e.g. *Kandelia* versus *Rhizophora*) and location of origin (*Avicennia* from India versus Australia). For example, the slowly-degrading leaves of *Rhizophora* contain more structural lignocellulose and less nitrogen than the more labile *Kandelia* leaves. Leaves of *K. candel* are also rich in total fatty acids, and in essential fatty acids (ω3 and ω6) entailing that they are of high nutritional quality (Mfilinge et al., 2005). The differential in elemental composition and degradability of litter from the same species between locations is probably related to the availability of nutrients in the environment. Interestingly, various aquatic plants from temperate environments (unicellular green algae and green macroalgae, as well as submerged vascular macrophytes and marsh grasses) also show an inverse relationship between elemental C:N ratio and decay constants

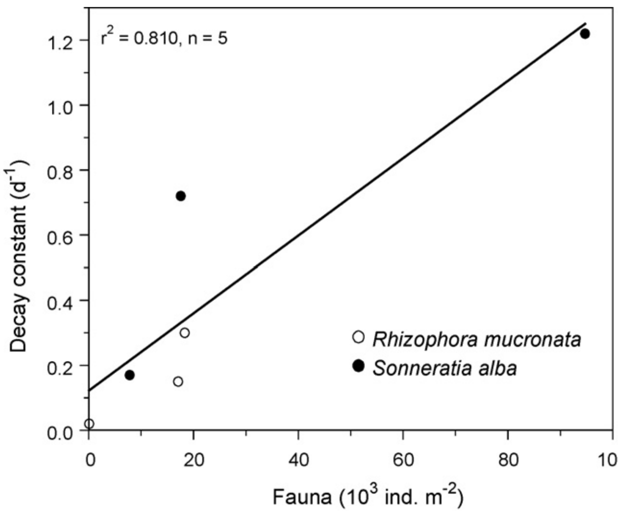

Fig. 3. Decay constants of *Rhizophora mucronata* and *Sonneratia alba* litter in litterbags as a function of benthic fauna abundance (including amphipods, nematodes, turbellarians, isopods and polychaetes, but excluding crabs). Data from Bosire et al. (2005).

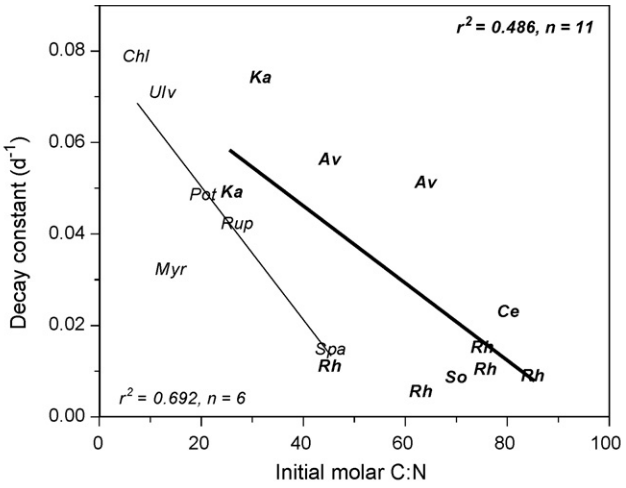

Fig. 4. Decay constants of a variety of mangrove litter (bold) and submerged macrophytes from temperate areas (light) as a function of the initial POC:TN ratio of the material. Least squares linear regression lines and correlation coefficients are shown for comparison (Twilley et al., 1986; Robertson, 1988; Twilley et al., 1997; Wafar et al., 1997; Tam et al., 1998; Mfilinge et al., 2002).

(Fig. 4). If the almost 10 °C difference in temperature between temperate and tropical incubations are considered and assuming a temperature dependence typical for biological processes (i.e. $Q_{10} \sim 2$–3), the two relationships are almost identical with nitrogen-rich algae decomposing fastest and nitrogen-poor mangrove litter decomposing slowest.

5.2. Sedimentary decomposition pathways

While the aerobic microbial community in mangrove environments consumes fresh litter and algal detritus deposited at or near the sediment surface, anaerobes are fuelled by detritus buried by accretion, by leaf-eating crabs and by belowground root production in the form of dead biomass and DOC excretions (Alongi, 1998; Kristensen and Alongi, 2006). Aerobic microorganisms have the enzymatic capacity for complete oxidation of organic carbon to CO_2, while anaerobic degradation processes occur stepwise involving several competitive types of prokaryotes. Aerobic degradation of labile materials near the surface of mangrove sediments is usually so rapid that O_2 rarely penetrates more than 2 mm into the sediment (Kristensen et al., 1994). The bulk sediment remains largely anoxic except for a network of narrow roots and infaunal burrows that translocate oxygen deep into the sediment (Kristensen and Alongi, 2006). Under anoxic conditions, large organic molecules are first split into small moieties by fermenting prokaryotes. These small molecules are then oxidized completely to CO_2 by a wide variety of anaerobic microorganisms using electron acceptors in the following sequence according to the energy yield: Mn^{4+}, NO_3^-, Fe^{3+} and SO_4^{2-}.

Aerobic respiration and anaerobic sulfate reduction are usually considered the most important respiration processes in mangrove sediments (Alongi, 1998), with a share of 40–50% each (Table 2). Consequently, most mangrove sediments contain high levels of reduced inorganic sulfur in the form of primarily pyrite (FeS_2) and elemental sulfur (S^0) and only negligible amounts of iron monosulfides (FeS) (Holmer et al., 1994). Denitrification, manganese respiration and iron respiration, on the other hand, have traditionally been considered unimportant in mangrove environments (Kristensen et al., 1998), although denitrification may be significant in areas impacted by sewage (Corredor and Morell, 1994). Recent evidence suggests, however, that the role of iron respiration in carbon oxidation may be comparable to, or higher than, sulfate reduction in iron-rich mangrove environments (Table 2). As sulfate reduction usually is hampered in the presence of more potent electron acceptors (e.g. O_2 and Fe^{3+}; Canfield et al., 2005), this process becomes inferior to iron respiration when oxidizing roots and infaunal burrows increase the Fe^{3+} content in mangrove sediments (Nielsen et al., 2003). Recent results have shown that the proportion of anaerobic respiration in mangrove sediments that is conducted via iron respiration (FeR) is significantly related to the concentration of reactive oxidized iron (Fe(III)) within the sediment (Fig. 5). Thus, when the concentration of reactive Fe(III) exceeds about 35 μmol cm^{-3}, more than 80% of the anaerobic carbon oxidation is mediated by microbial iron reduction. This relationship is strikingly similar to that generally found for other marine areas (Jensen et al., 2003).

When all electron acceptors are exhausted and electron donors are in surplus, CH_4 is produced by fermentative disproportionation of low molecular compounds (e.g. acetate) or reduction of CO_2 by hydrogen or simple alcohols (Canfield et al., 2005). Thus, a process like sulfate reduction can usually maintain concentrations of hydrogen and acetate at levels too low to fuel methanogens. In general, rates of methane production are low and highly variable in mangrove sediments, and in some environments the process cannot be detected at all (Alongi et al., 2004, 2005b). Despite the presence of active methanogenesis, the concentration of methane in porewaters of near-surface sediments is usually very low due to simultaneous removal by anaerobic methane oxidation (Canfield et al., 2005). Emissions of methane from mangrove sediments are therefore close to zero (range from 0 to 5 mmol m^{-2} d^{-1}). There is a general consensus that anthropogenic influence, i.e. higher nutrient and organic loading, strongly increases emissions of methane from mangrove sediments by inducing severe oxygen stress and supplying labile organic carbon (Giani et al., 1996; Purvaja and Ramesh, 2001; Kreuzwieser et al., 2003; Alongi et al., 2005b). Nevertheless, our knowledge on factors controlling methanogenesis and methane emissions in mangrove environments is limited and relies primarily on a few recent studies.

Rates of microbial carbon oxidation and partitioning of electron acceptors within typical marine sediments are usually dependent on the quantity and reactivity of organic matter, sediment grain size, and bioturbation activity (Kristensen, 2000). However, in mangrove sediments other factors are equally important; these include forest age, physiological activities of the root system, extent of water logging and

Table 2
Total carbon oxidation (tot C-ox) measured as benthic CO_2 release and partitioning of electron acceptors in mangrove sediments

Location	Tot C-ox	NO_3^-	Mn(IV)	Fe(III)	SO_4^{2-}	CH_4 prod	References
Bangrong, Thailand	32–62	<0.1[a]	n.m.	17–36	5–10	n.m.	1
Ao Nam Bor, Thailand	54–190	n.m.	n.m.	n.m.	20–46	n.m.	2
Mekong Delta, Vietnam	17–54	0–4	0.5–1.4	<0.1[b]	2–15	~0	3
Matang, Malaysia	77–102	8–19	n.m.	n.m.	39–88	~0	4
Jiulongjiang, China	67–79	2–8	1–18	0–11[b]	162–562	<0.1	5
Pichavaram, India	106–190	n.m.	1–39	1–11[b]	42–638	n.m.	6
Indus Delta, Pakistan	47–50	n.m.	n.m.	n.m.	23–32	n.m.	7
Port Hedland, Australia	28–48	n.m.	<0.1	<0.1[b]	11–53	~0	8
Dampier, Australia	37–51	n.m.	<0.1	~0[b]	7–28	~0	8
Mangrove Bay, Australia	29	n.m.	~0	~0[b]	16	~0	8
Bay of Rest, Australia	33	n.m.	<0.1	0.1[b]	46	~0	8
Haughton, Australia	40–93	n.m.	n.m.	21–64	14–24	n.m.	9
Hinchinbrook, Australia	2–22	6–14	<0.1	~0[b]	2–20	~0	10
Mtoni, Tanzania	55–107	n.m.	n.m.	27–49	4–6	n.m.	11
Ras Dege, Tanzania	73–79	n.m.	n.m.	35–57	11–46	n.m.	11
Gazi Bay, Kenya	55–373	n.m.	n.m.	n.m.	n.m.	n.m.	12

The contribution (in C units) by independently measured anaerobic microbial carbon oxidation processes using various electron acceptors are given. Units are mmol C m^{-2} d^{-1} (n.m.—not measured) (modified from Kristensen, 2007). References: (1) Kristensen et al. (2000); (2) Kristensen et al. (1994); (3) Alongi et al. (2000a); (4) Alongi et al. (2004); (5) Alongi et al. (2005b); (6) Alongi et al. (2005c); (7) Kristensen et al. (1992); (8) Alongi et al. (2000b); (9) Kristensen and Alongi (2006); (10) Alongi et al. (1999); (11) Kristensen (unpublished); (12) Middelburg et al. (1996).

[a] Obtained from the nearby Ao Nam Bor mangrove forest (Kristensen et al., 1998).

[b] Estimated from the generation of dissolved Fe^{2+} only, and thereby ignoring generation of solid Fe(II).

intensity of faunal burrowing activities. It has been observed that sulfate reduction accounts for 20–30% in young *Avicennia marina* and *Rhizophora apiculata* forests, while this process is responsible for most carbon oxidation in old forests (Alongi et al., 1998, 2000a). Oxidized conditions with dominance of aerobic and iron respiration prevail in sediments beneath young *Rhizophora* stands characterized by low plant biomass and high exposure to tidal effect on well-aerated sandy substratum. As forests age, the organic carbon input becomes stronger, and the increasing amount of fresh organic matter leads to a prevalence of sulfate reduction. The effect of *Avicennia marina* roots on sediment biogeochemistry, on the other hand, appears contradictive. Oxygen leaching by roots keeps the rhizosphere deep in the sediment oxidized and enriched in Fe(III) for use by iron reducers. At the same time, leaching of labile DOC from roots appears to stimulate bulk sulfate reduction (Kristensen and Alongi, 2006). The impact of water logging is evident in mature *Avicennia* forests. When the water table is low during the dry season, oxygen penetrates deeper into the sediment through crab burrows and cracks in the sediment and adds to the oxidizing effect of the rhizosphere, allowing suboxic (e.g. iron reduction) oxidation of organic carbon. Conversely, during the rainy season, prolonged water logging prevents oxidation of the sediment and sulfate reduction becomes the dominant pathway (Clark et al., 1998; Marchand et al., 2004). Animal burrows are a major conduit for subsurface movement of water (Ridd, 1996). They allow the supply of oxygen and oxidized elements below the depth at which oxygen usually penetrate, resulting in the development of oxidized halos around burrows (Clark et al., 1998). Thus, Kristensen et al. (2000) observed that sulfate reduction in a burrowed mudflat is reduced to half of that in adjacent vegetated and almost fauna-free sediments.

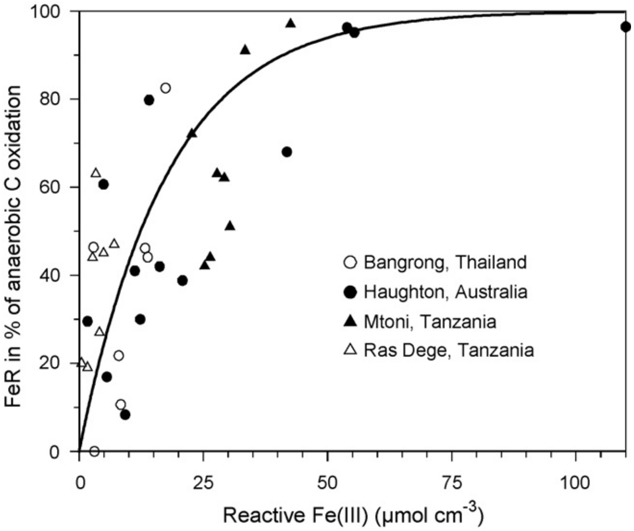

Fig. 5. Relationship between the proportion of iron respiration (FeR) to total anaerobic carbon oxidation in mangrove sediments and the corresponding concentration of reactive Fe(III). Data are from Thailand (Kristensen et al., 2000); Australia (Kristensen and Alongi, 2006) and Tanzania (Kristensen, unpublished). Full line shows the best fit with a constant $a = 0.044$ to the equation %FeR = 100 (1 − exp(−a Fe(III))).

5.3. Rates of sedimentary carbon oxidation

The total sediment metabolism, which can be quantified as dark CO_2 release, represents the sum of all aerobic and anaerobic respiration processes and provide an estimate of the total decomposition occurring within the sediment. Based on the available data, the global average release of CO_2 from mangrove sediments in the dark is roughly 27 mol m^{-2} $year^{-1}$ (equivalent to 75 mmol m^{-2} d^{-1} and covering a range from 2 to 373 mmol m^{-2} d^{-1}) (Table 2). Most of these highly variable rates are probably seriously underestimated as they generally are based on flux measurements of inundated and air-exposed bare sediment away from trees and burrows. Recent measurements have shown, however, that air-exposed pneumatophores and open crab burrows increase CO_2 emissions to the atmosphere considerably by efficient translocation of CO_2 gas from deeper sediments. Thus, Kristensen (unpublished) found that the contribution of 100 *Sonneratia alba* pneumatophores m^{-2} is about 170 mmol CO_2 d^{-1} and 100 *Avicennia marina* pneumatophores m^{-2} is roughly 60 mmol CO_2 d^{-1}, while 100 *Uca* spp. burrows m^{-2} may add 90 mmol CO_2 d^{-1} to the basic rate measured for bare sediment. In addition, respiration by the crabs themselves also contributes to CO_2 loss from the sediment. A biomass of 250 g ww *Uca* spp. respires 16 mmol CO_2 d^{-1} (Kristensen, unpublished) and the same biomass of sesarmids (*Neoepisesarma versicolor*) respires 21 mmol CO_2 d^{-1} (Thongtham and Kristensen, 2005). It is therefore important that future studies on sediment metabolism in mangrove environments quantify the abundance of aerial roots and crab burrows (including crabs) and contain their contribution into the efflux of CO_2 to provide reliable estimates of carbon oxidation in mangrove sediments. Such estimates may prove essential for obtaining trustworthy global carbon budgets.

6. Burial and permanent storage of organic carbon in sediments

Mangrove ecosystems are able to store large amounts of organic carbon (Matsui, 1998; Fujimoto et al., 1999) and in some mangrove ecosystems, organic-rich sediments of several meters depth have been found (Twilley et al., 1992; Lallier-Verges et al., 1998). The formation of old and refractory material in mangrove sediments can be observed visually as lignified and humified (spongy) litter fragments. Accordingly, Dittmar and Lara (2001b) estimated that the average age of organic carbon in the upper 1.5 m of the sediment in the Furo do Meio mangrove forest, Brazil is between 400 and 770 years. Based on a compilation of available data, Duarte and Cebrián (1996) estimated that ~10% of the mangrove production is buried in the sedimentary pool, the remainder being exported (~30%), consumed (~9%), decomposed (~40%), or unaccounted (10%). However, the percentage of buried carbon strongly depends on the environmental conditions. As primary production increases with stand age, the efficiency of carbon burial in sediments increases, from 16% for a 5-year-old forest to 27% for an 85-year-old stand (Alongi et al., 2004). Additionally, there is proportionally greater carbon burial in the low intertidal zone where sediment accumulation is greatest (Alongi et al., 2005b). Duarte et al. (2005) recently estimated the average global rate of carbon accumulation in mangrove systems at 10.8 mol m^{-2} $year^{-1}$, which is similar to the 10.7 mol m^{-2} $year^{-1}$ estimated by Jennerjahn and Ittekkot (2002). There are, however, a number of caveats in such global estimates and it will likely require substantially more data to be able to constrain these budgets better.

The available global estimates of carbon accumulation are mainly calculated by difference using litter fall, export and consumption rates (Jennerjahn and Ittekkot (2002) and many of the case studies used in the approach of Duarte and Cebrián (1996)). This approach does not emphasize the fact that NPP is likely to be three to four-fold higher than the litter fall rates, which may lead to a significant underestimate of burial rates. Also, other potentially important organic carbon sources derived from tidal water, such as seagrass detritus, phytodetritus and terrestrial material (Bouillon et al., 2003; Marchand et al., 2003; Kennedy et al., 2004) are usually not considered in accumulation estimates, which may further accentuate the underestimate of carbon burial rates.

From that perspective, direct measurements of sediment and/or carbon accumulation rates hold a better potential, but unfortunately the number of such data are scarce (Chmura et al., 2003; Duarte et al., 2005) which raises the question as to whether these are representative enough for a global extrapolation. Looking into the datasets used by Duarte et al. (2005), the sediment carbon content of the mangrove sites considered was 8.5%, whereas a more exhaustive data compilation indicates that a representative global estimate of carbon content is likely to be close to 2.2% (Fig. 2), suggesting that the data used in this bottom-up approach is biased towards organic-rich systems and hence overestimates the global carbon accumulation in mangroves.

The close match between different approaches (Twilley et al., 1992 and references cited above) is therefore remarkable—although this does not need to imply that the carbon burial rate is well constrained, and more data need to be generated before this estimate can be confirmed or improved.

7. Outwelling and dispersal of mangrove organic matter

About four decades ago, Odum (1968) proposed a groundbreaking hypothesis in coastal ecology according to which the outwelling of litter from coastal wetlands is a major source of energy that supports much of the secondary production of estuaries and nearshore waters. Because of the regular tidal flooding and draining in most mangrove areas, the material exchange between the forests and coastal waters can be very efficient (e.g. Dittmar and Lara, 2001a). Many of the most productive mangrove forests in the world lose a significant fraction of their net primary production to coastal waters (Robertson et al., 1992; Jennerjahn and Ittekkot, 2002). Large differences occur between mangrove forests with respect to litter production and export rates, and some largely retain detritus within their sediments (Woodroffe, 1992), which is then mineralized or buried. On a global average, however, numerous studies indicate that mangrove forests are a significant net-source of detritus to adjacent coastal water, and the global export rate of mangrove litter has been estimated to be 19 mol C m^{-2} $year^{-1}$ which is approximately half of the total litter production (Jennerjahn and Ittekkot, 2002).

While there are clear patterns of high particulate detritus export in most mangrove environments, the utilization of this organic matter in marine food webs seems inconsistent. The large flux of mangrove detritus to the coastal ocean can have recognizable effects on aquatic food webs in some areas (Odum and Heald, 1975; Alongi et al., 1989; Alongi, 1990), but the litter outwelling hypothesis has been challenged in other areas (Lee, 1995; Schwamborn et al., 1999). Some studies show that, as far as particulate organic matter fluxes are concerned, mangrove forests and adjacent environments can strongly interact. For example, Hemminga et al. (1994) observed a tight coupling between mangrove forests and seagrass meadows in Gazi Bay (Kenya) where strong outwelling of particles from the mangrove environment is evident. During flood tides, however, reversed transport of organic particles from the seagrass zone to the mangrove forest can be observed. Respiratory CO_2 derived from mangrove detritus can be a major inorganic carbon source for the seagrass meadows as observed by Hemminga et al. (1994) in Gazi Bay, Kenya, and Lin et al. (1991) for a mangrove-seagrass system in Florida. In contrast to the tight coupling between mangroves and adjacent seagrasses, particle outwelling is often restricted to the reef line (Schwamborn et al., 1999) while nearby coral reefs can exist in relative isolation from mangrove influence (Hemminga et al., 1994). Thus, the role of mangrove litter on sediment processes and the tight coupling with adjacent ecosystems is mostly restricted to the direct vicinity of the forests. A few kilometers offshore, however, mangrove litter usually contributes insignificantly to the organic matter accumulating in sediments or to the carbon consumed by organisms (Hemminga et al., 1994; Jennerjahn and Ittekkot, 2002).

Two major processes can explain the lack of a significant offshore impact of litter outwelling. (1) The distribution of exported mangrove litter largely depends on the local geomorphology and hydrodynamics. Many mangrove forests fringe semi-enclosed bays and estuaries. Water currents within these settings can efficiently trap suspended particles (Jay and Musiak, 1994) and cause enhanced sedimentation rates in direct vicinity of the mangrove environment. Lithogenic input from rivers can provide mineral ballast for the production of fast-sinking aggregates (Jennerjahn et al., 1999). Large-scale boundary currents can also diminish the dispersion of terrigenous suspended particles off the continental margins (Jennerjahn and Ittekkot, 2002). (2) On the time-scale of outwelling, a significant fraction of litter is lost as dissolved organic carbon (DOC). Within the first weeks of litter degradation in the water column or submersed sediments, >75% of organic carbon can be lost (Dittmar and Lara, 2001b; Schories et al., 2003), most of it to the dissolved pool (Benner et al., 1990; Wafar et al., 1997).

Mangrove-derived DOC is also released into the water column through the tidal pumping of DOC-rich porewaters, which can significantly add to the total organic carbon export (Bouillon et al., 2007b). DOC concentrations in mangrove porewaters varies considerably within and among forests, but levels as high as 9 mmol L^{-1} has been recorded (Marchand et al., 2006). Quantitative estimates from mangrove forests around the world almost consistently indicate that a significant fraction of the net carbon fixation through primary production is indeed exported to coastal waters as DOC (Boto and Wellington, 1988; Dittmar et al., 2006). Decomposition and leaching products of leaf litter are likely sources of the exported mangrove-DOC (Dittmar et al., 2001), while the contribution of root exudates or decomposing below-ground biomass is not known. The total export rate of organic carbon from mangrove forests may significantly exceed the estimates of litter export by Jennerjahn and Ittekkot (2002; 19 mol C m^{-2} $year^{-1}$) if the export of DOC is taken into account. Tidal DOC export from a Florida mangrove area (Twilley, 1985) was estimated to be 3.1–3.7 mol C m^{-2} $year^{-1}$, while a mangrove tidal creek in Australia (Ayukai et al., 1998) exports 1.8 mol C m^{-2} $year^{-1}$, and a mangrove forest in Thailand loses 0.6 mol C m^{-2} $year^{-1}$ (Suraswadi, unpublished). These export estimates are usually based on small-scale studies performed within or in direct vicinity of the mangroves. The only study performed so far on a continental-shelf scale (Dittmar et al., 2006) indicates a significantly higher outwelling of DOC (12 mol C m^{-2} $year^{-1}$) compared to previous small-scale studies in the same region in northern Brazil (4 mol C m^{-2} $year^{-1}$; Dittmar et al., 2001) or elsewhere in the world. The reason behind this discrepancy is probably that the gradual release of DOC from floating and suspended detritus in the water column was not accounted for in past studies. From the well-developed mangrove forest in Brazil about 13 mol C m^{-2} $year^{-1}$ of floating debris were exported through tidal creeks over the course of an annual sampling campaign (Schories et al., 2003). In addition to floating debris, suspended solids (POC) were exported at a rate of 3 mol C m^{-2} $year^{-1}$ (Dittmar and Lara, 2001a,c). Stable carbon isotope and lignin analyses indicated leaf litter as the primary source of the exported POC (Dittmar et al., 2001). The combined export of debris and POC accounts for ~40% of the total litter fall in this mangrove forest. Mangrove-derived dissolved organic carbon (DOC) is exported at a rate of 4 mol C m^{-2} $year^{-1}$ (Dittmar and Lara, 2001c). The combined export for all organic matter fractions (debris, POC, and DOC) is 20 mol C m^{-2} $year^{-1}$. A major fraction (12 mol C m^{-2} $year^{-1}$) of this organic matter is ultimately transported across the shelf in form of DOC, probably after extensive photochemical and microbial reworking (Dittmar et al., 2006).

The release of DOC from mangrove compartments causes pronounced tidal signatures. For example, DOC concentrations in a tidal creek in northern Brazil that drains a well-developed mangrove area showed a pronounced tidal pattern (Dittmar and Lara, 2001a; Fig. 6). During ebb, DOC-rich porewater seeps out of the mangrove sediments and the concentrations sharply increase. The molecular lignin signature of this DOM showed that degradation products of mangrove detritus (mainly *R. mangle* and *A. germinans* litter) are the main source of DOC seeping out of the sediments (Dittmar et al., 2001). In a very similar fashion, DOC concentrations were found to fluctuate according to the tides in a pristine mangrove creek in Tanzania

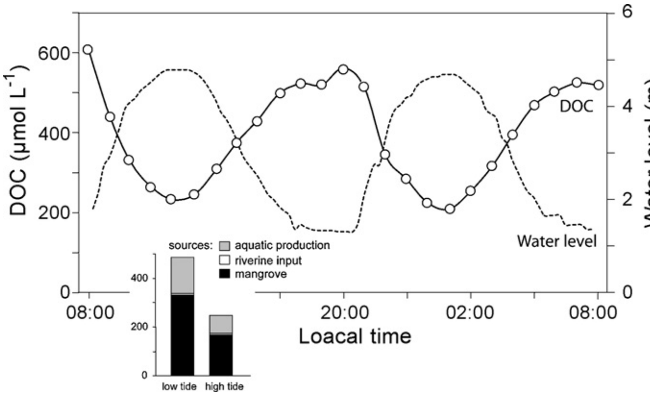

Fig. 6. An example of a 24-h time-series of DOC and water level in a tidal creek that drains about 2.2 km^2 of a well-developed mangrove forest in tropical Brazil (Bragança) during the rainy season (29–30 May, 1997; Dittmar and Lara, 2001a). Source assignment of DOC was made with a molecular lignin approach (Dittmar et al., 2001). Annual average values ($n = 17$) are shown for low and high tide.

(Fig. 7; Bouillon et al., 2007b). There, two major sources of DOM could be distinguished. The stable carbon isotope composition of DOC closely followed the tidal cycle, and indicated inputs of ^{13}C-enriched (seagrass) material into the mangrove during flood tide, and ^{13}C-depleted mangrove DOM leaving the system during ebb tide.

Important master variables that control to a large degree the magnitude of organic matter outwelling and the partition between debris, POC and DOC outwelling are net primary production, the abundance of litter-collecting fauna and tidal range. In the mangrove forest of Bragança (northern Brazil), the leaf-removing crab *Ucides cordatus* has a key-role for leaf-litter turnover, significantly impacting litter export and decomposition (Schories et al., 2003). The main vehicle for DOC outwelling is tidally induced porewater flow from the upper sediment and litter horizon (Dittmar and Lara, 2001a) which is largely controlled by tidal range.

Little is known about the fate of mangrove-derived DOC in the ocean. The bulk of the leachable fraction from *R. mangle* leaves can be mineralized rapidly and assimilated into microbial biomass (Benner and Hodson, 1985). A significant fraction of mangrove-derived DOC, however, is relatively resistant to degradation. Photodegradation and bio-incubation experiments indicate that a substantial fraction (∼50%) of the DOC in mangrove porewater is refractory on a time-scale of weeks to years. Thus, it may be distributed over larger distances on continental shelves and beyond, depending mainly on the local hydrodynamics at the sites of export. Slow mineralization of mangrove-DOC could fuel aquatic (secondary) production far away from the mangrove areas, giving reason to revive the original outwelling hypothesis in a modified form. On the North Brazil Shelf, mixing diagrams (Fig. 8a) indicate a strong brackish water source of DOC. Stable carbon isotope analyses confirm that mangroves, including microbial secondary products, are the prime source of this DOC (Dittmar et al., 2006). Mangrove-derived DOC is present on the North Brazil Shelf at distances >100 km offshore. Mixing diagrams from a mangrove-fringed creek in Tanzania show a strong source of DOC at high salinity (Fig. 8b; Bouillon et al., 2007b), i.e. due to highly saline porewater intrusion at low tide and sediment-water exchange during tidal inundation. Mangrove-derived DOC in this porewater appeared to mix conservatively with low-DOC waters, which suggests a refractory nature of mangrove-DOC in this system over the time frame of the water residence time (estimated at 2–3 days, M.R. Flindt, pers. comm.). Refractory properties are a prerequisite for further dispersion on continental shelves.

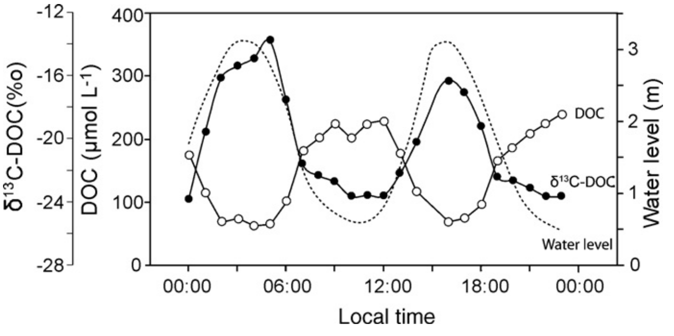

Fig. 7. Example of 24-h time-series of DOC, δ^{13}C of DOC and water level in a tidal creek that drains about 2.2 km^2 of a pristine mangrove forest (Ras Dege) in Tanzania during the dry season (16–17 September, 2005) (Bouillon et al., 2007b).

Mangroves probably contribute >10% of the terrestrially-derived, refractory DOC transported to the ocean (Dittmar et al., 2006), while they cover only <0.1% of the continents' surface. Organic carbon export from mangrove areas to the ocean is more than one order of magnitude higher in proportion to their net-primary production than any major river (Fig. 9). The rapid decline in mangrove cover over the recent decades (Valiela et al., 2001) may have significantly impacted the flux of terrigenous DOC to the ocean.

8. Perspectives and research directions

Over the past two decades, a large number of case studies have significantly increased our knowledge on carbon dynamics in mangrove systems and on the importance of various biogeochemical processes. We still lack, however, a complete understanding of the underlying mechanisms controlling the spatial and temporal variability of these processes as a function of changes in environmental conditions. Vegetation type, faunal composition, microbial processes and sediment structure changes along tidal elevation gradients, and range from more marine influenced communities near the seaward edge to a significant terrestrial imprint at the higher elevations (hundreds of meter to kilometre scales). The variability in carbon transformations and transport conditions among mangrove environments is affected by specific local conditions with respect to climate, degree of exposure to strong water movement, the vicinity of river discharges, soil and bedrock composition in the neighboring terrestrial system and, not the least, the local vegetation and fauna. Due to such inherent environmental variability combined with the rather limited data available, generalizations on a global scale become

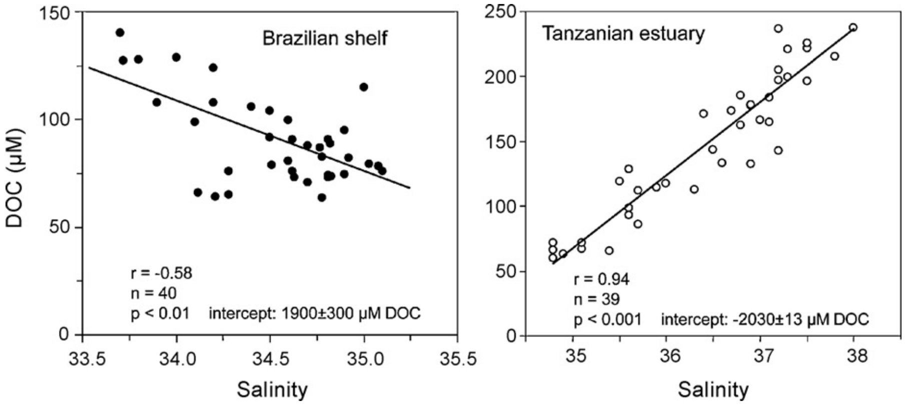

Fig. 8. Mixing diagrams of DOC concentrations on the mangrove-fringed North Brazilian shelf (October–November 2001; Dittmar et al., 2006) and a mangrove tidal creek in Tanzania (Ras Dege; September 2005; Bouillon et al., 2007b).

troublesome, and future progress can only be made by significantly increasing the spatial and temporal components of our database.

The characterization of the molecular composition of mangrove tissues (and other organic matter sources) has been much refined, and the further development of tracer techniques combined with molecular and isotope approaches can therefore be expected to offer exciting opportunities to trace mangrove-derived organic matter in much more detail than was previously possible. This should contribute to our understanding of past ecosystem changes as well as the functioning of contemporary mangrove systems. However, in order to better constrain mangrove carbon budgets and the impact of mangroves on the coastal ocean, a better appraisal of mangrove net primary productivity is crucial, in particular a more robust set of data on wood and belowground production. Additionally, more studies on organic matter preservation (e.g. incorporation of sulfur within the organic matter or adsorption onto clay minerals) are needed to better constrain the type of organic matter that is buried in mangrove sediments and to allow for a more precise interpretation of sediment core data to reconstruct past mangrove environments.

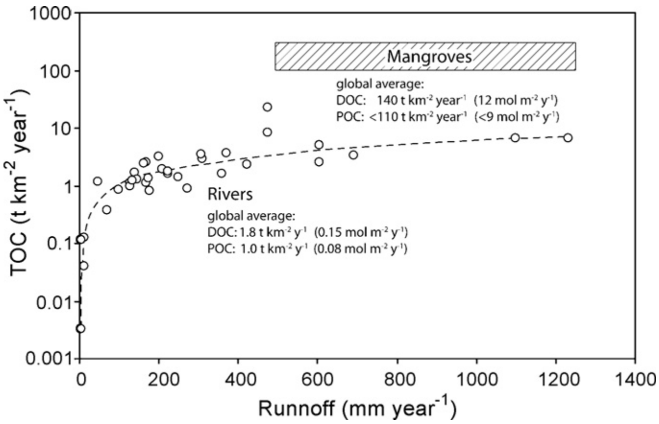

Fig. 9. Comparison between the area-normalized organic carbon runoff from mangrove forests (DOC: Dittmar et al., 2006) and major world rivers (Spitzy and Leenheer, 1991) from all climate zones draining a variety of continental biomes. POC export rates from mangrove forests assume that more than 50% of the reported litter export (Jennerjahn and Ittekkot, 2002) is rapidly lost to the DOC pool and/or assimilated and not exported as suspended or floating matter off the inner-coastal zone (see text for details).

Mangrove ecosystems are being converted or degraded at alarming rates, and we have already witnessed major losses worldwide. Given the high potential impact of mangroves on sedimentation of riverine suspended matter, and on exchange of organic matter and nutrients with coastal waters, such high losses or severe degradation of their functioning can be expected to coincide with important changes in coastal zone carbon budgets. Efforts to conserve and restore mangrove forests are being conducted in many different areas, and one important aspect in assessing the success of these efforts is to verify the extent to which restored or replanted sites function similarly to pristine sites, both in terms of their habitat function for faunal communities (e.g., Bosire et al., 2004, 2008), and in terms of their productivity and biogeochemical functioning (McKee and Faulkner, 2000; Bosire et al., 2005). A sound knowledge on biogeochemical processes and the factors influencing carbon dynamics in natural systems is of prime importance in enabling a proper evaluation of the restoration success (McKee and Faulkner, 2000; Bosire et al., 2008). Mangroves are also under increasing stress from anthropogenic pollution and nutrient inputs, and have been considered efficient systems for the removal of nutrients and other anthropogenic pollutants (e.g., Tam and Wong, 1993). Here, too, a more fundamental understanding of nutrient cycling and factors influencing the nutrient processing pathways will be important in enabling us to determine the carrying capacity of these ecosystems and the long-term response to inevitable further increased inputs of nutrients in tropical coastal ecosystems.

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References

Aké-Castillo, J., Vázquez, G., López-Portillo, J., 2006. Litterfall and decomposition of *Rhizophora mangle* L. in a coastal lagoon in the southern Gulf of Mexico. Hydrobiologia 559, 101–111.

Alfaro, A.C., Thomas, F., Sergent, L., Duxbury, M., 2006. Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. Estuar. Coast. Shelf Sci. 70, 271–286.

Alongi, D.M., 1990. Abundances of benthic microfauna in relation to outwelling of mangrove detritus in a tropical coastal region. Mar. Ecol. Prog. Ser. 63, 53–63.

Alongi, D.M., 1994. Zonation and seasonality of benthic primary production and community respiration in tropical mangrove forests. Oecologia 98, 320–327.

Alongi, D.M., 1998. Coastal Ecosystem Processes. CRC Press, p. 419.

Alongi, D.M., 2007. The contribution of mangrove ecosystems to global carbon cycling and greenhouse gas emissions. In: Tateda, Y., Upstill-Goddard, R., Goreau, T., Alongi, D., Nose, A., Kristensen, E., Wattayakorn, G. (Eds.), Greenhouse Gas and Carbon Balances in Mangrove Coastal Ecosystems. Maruzen, Tokyo, pp. 1–10.

Alongi, D.M., Boto, K.G., Tirendi, F., 1989. Effect of exported mangrove litter on bacterial productivity and dissolved organic carbon fluxes in adjacent tropical nearshore sediments. Mar. Ecol. Prog. Ser. 56, 133–144.

Alongi, D.M., Clough, B.F., Robertson, A.I., 2005a. Nutrient-use efficiency in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. Aquat. Bot. 82, 121–131.

Alongi, D.M., Dixon, P., 2000. Mangrove primary production and above and below-ground biomass in Sawi Bay, southern Thailand. Phuket Mar. Biol. Center. Spec. Publ. 22, 31–38.

Alongi, D.M., Tirendi, F., Trott, L.A., Xuan, T.T., 2000a. Benthic decomposition rates and pathways in plantations of the mangrove *Rhizophora apiculata* in the Mekong delta. Vietnam Mar. Ecol. Prog. Ser. 194, 87–101.

Alongi, D.M., Pfitzner, J., Trott, L.A., Tirendi, F., Dixon, P., Klumpp, D.W., 2005b. Rapid sediment accumulation and microbial mineralization in forests of the mangrove Kandelia candel in the Jiulongjiang Estuary, China. Estuar. Coast. Shelf Sci. 63, 605–618.

Alongi, D.M., Ramanathan, A.L., Kannan, L., Tirendi, F., Trott, L.A., Bala Krishna Prasad, M., 2005c. Influence of human-induced disturbance on benthic microbial metabolism in the Pichavaram mangroves, Vellar-Coleroon complex, India. Mar. Biol. 147, 1033–1044.

Alongi, D.M., Sasekumar, A., Tirendi, F., Dixon, P., 1998. The influence of stand age on benthic decomposition and recycling of organic matter in managed mangrove forests of Malaysia. J. Exp. Mar. Biol. Ecol. 225, 197–218.

Alongi, D.M., Sasekumar, A., Chong, V.C., Pfitzner, J., Trott, L.A., Tirendi, F., Dixon, P., Brunskill, G.J., 2004. Sediment accumulation and organic material flux in a managed mangrove ecosystem: estimates of land–ocean–atmosphere exchange in peninsular Malaysia. Mar. Geol. 208, 383–402.

Alongi, D.M., Tirendi, F., Clough, B.F., 2000b. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. Aquat. Bot. 68, 97–122.

Alongi, D.M., Tirendi, F., Dixon, P., Trott, L.A., Brunskill, G.J., 1999. Mineralization of organic matter in intertidal sediments of a tropical semi-enclosed delta. Estuar. Coast. Shelf Sci. 48, 451–467.

Ayukai, T., Miller, D., Wolanksi, E., Spagnol, S., 1998. Fluxes of nutrients and dissolved and particulate organic matter in two mangrove creeks in north-eastern Australia. Mangr. Salt Marshes 2, 223–230.

Benner, R., Hodson, R.E., 1985. Microbial degradation of the leachable and lignocellulosic components of leaves and wood from *Rhizophora mangrove* in a tropical mangrove swamp. Mar. Ecol. Prog. Ser. 23, 221–230.

Benner, R., Weliky, K., Hedges, J.I., 1990. Early diagenesis of mangrove leaves in a tropical estuary: molecular-level analyses of neutral sugars and lignin derived phenols. Geochim. Cosmochim. Acta 54, 1991–2001.

Benner, R., Peele, E.R., Hodson, R.E., 1986. Microbial utilization of dissolved organic matter from leaves of the Red Mangrove, Rhizophora mangle, in the Fresh creek estuary. Bahamas Estuar. Coast. Shelf Sci. 23, 607–619.

Borges, A.V., Djenidi, S., Lacroix, G., Théate, J., Delille, B., Frankignoulle, M., 2003. Atmospheric CO_2 flux from mangrove surrounding waters. Geophys. Res. Lett. 30, 1558.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Kazungu, J., Dehairs, F., Koedam, N., 2005. Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya. Biol. Conserv. 126, 287–295.

Bosire, J., Dahdouh-Guebas, F., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay. Biodiv. Conserv. 13, 1059–1074.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

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. Prog. Ser. 50, 151–160.

Boto, K.G., Alongi, D.M., Nott, A.L.J., 1989. Dissolved organic carbon–bacteria interactions at sediment-water interface in a tropical mangrove system. Mar. Ecol. Prog. Ser. 51, 243–251.

Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130, 441–448.

Bouillon, S., Dahdouh-Guebas, F., Rao, A.V.V.S., Koedam, N., Dehairs, F., 2003. Sources of organic carbon in mangrove sediments: variability and possible ecological implications. Hydrobiologia 495, 33–39.

Bouillon, S., Moens, T., Overmeer, I., Koedam, N., Dehairs, F., 2004. Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. Mar. Ecol. Prog. Ser. 278, 77–88.

Bouillon, S., Dehairs, F., Schiettecatte, L.-S., Borges, A.V., 2007a. Biogeochemistry of the Tana estuary and delta (northern Kenya). Limnol. Oceanogr. 52, 46–59.

Bouillon, S., Middelburg, J.J., Dehairs, F., Borges, A.V., Abril, G., Flindt, M., Ulomi, S., Kristensen, E., 2007b. Importance of intertidal sediment processes and porewater exchange on the water column biogeochemistry in a pristine mangrove creek (Ras Dege, Tanzania). Biogeosciences 4, 311–322.

Bouillon, S., Connolly, R., and Lee, S.Y., 2008. Carbon exchange and cycling in mangrove ecosystems: a synthesis of recent insights based on stable isotope studies, J. Sea Res., doi:10.1016/j.seares.2007.05.001, in press.

Branch, G.M., Branch, M.L., 1980. Competition in *Bembicium auratum* (Gastropoda) and its effect on microalgal standing stocks in mangrove muds. Oecologia 46, 106–114.

Camilleri, J.C., Ribi, G., 1986. Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes from DOC, and feeding on flakes by crustaceans in mangroves. Mar. Biol. 91, 337–344.

Canfield, D.E., Kristensen, E., Thamdrup, B., 2005. Aquatic Geomicrobiology. Elsevier, Amsterdam, p. 640.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., Lynch, J.C., 2003. Global carbon sequestration in tidal, saline wetland soils. Glob. Biogeochem. Cycles 17 (4), 1111.

Clark, M.W., McConchie, D., Lewis, D.W., Saenger, P., 1998. Redox stratification and heavy metal partitioning in *Avicennia*-dominated mangrove sediments: a geochemical model. Chem. Geol. 149, 147–171.

Corredor, J.E., Morell, J.M., 1994. Nitrate depuration of secondary sewage effluents in mangrove sediments. Estuaries 17, 295–300.

Dahdouh-Guebas, F., Giuggioli, M., Oluoch, A., Vannini, M., Cannicci, S., 1999. Feeding habits of non-ocypodid mangrove crabs from Kenya. Bull. Mar. Sci. 64, 291–297.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Koedam, N., 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347, 83–89.

Day, J.W., Connor, W.H., Leylou, F., Day, R.H., Navarro, A.M., 1987. The productivity and composition of mangrove forests, Laguna de Terminos, Mexico. Aquat. Bot. 27, 267–284.

Dittmar, T., Lara, R.J., 2001a. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in north Brazil. Estuar. Coast. Shelf Sci. 52, 249–259.

Dittmar, T., Lara, R.J., 2001b. Molecular evidence for lignin degradation in sulfate reducing mangrove sediments (Amazônia, Brazil). Geochim. Cosmochim. Acta 65, 1403–1414.

Dittmar, T., Lara, R.J., 2001c. Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River? Evidence from long-term flux measurements. Mar. Ecol. Prog. Ser. 213, 67–77.

Dittmar, T., Lara, R.J., Kattner, G., 2001. River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Mar. Chem. 73, 253–271.

Dittmar, T., Hertkorn, N., Kattner, G., Lara, R.J., 2006. Mangroves, a major source of dissolved organic carbon to the oceans. Glob. Biogeochem. Cycles 20 , doi:10.1029/2005GB002570.

Dodd, R.S., Fromard, F., Rafii, Z.A., Blasco, F., 1995. Biodiversity among west African *Rhizophora*: foliar wax chemistry. Biochem. System. Ecol. 23, 859–868.

Dodd, R.S., Rafii, Z.A., Fromard, F., Blasco, F., 1998. Evolutionary diversity among Atlantic coast mangroves. Acta Oecol. 19, 323–330.

Dodd, R.S., Blasco, F., Rafii, Z.A., Torquebiau, E., 1999. Mangroves of the United Arab Emirates: ecotypic diversity in cuticular waxes at the bioclimatic extreme. Aquat. Bot. 63, 291–304.

Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41, 1758–1766.

Duarte, C.M., Middelburg, J.J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2, 1–8.

Dye, A.H., Lasiak, T.A., 1986. Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. Mar. Ecol. Prog. Ser. 32, 259–267.

Dye, A.H., Lasiak, T.A., 1987. Assimilation efficiencies of fiddler crabs and deposit-feeding gastropods from tropical mangrove sediments. Comp. Biochem. Physiol. 87A, 341–344.

Emmerson, W.D., McGwynne, L.E., 1992. Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. J. Exp. Mar. Biol. Ecol. 157, 41–53.

Fratini, S., Cannicci, S., Vannini, M., 2000. Competition and interaction between *Neosarmatium meinerti* (Crustacea: Grapsidae) and *Terebralia palustris* (Mollusca: Gastropoda) in a Kenyan mangrove. Mar. Biol. 137, 309–316.

Fujimoto, K., Imaya, A., Tabuchi, R., Kuramoto, S., Utsugi, H., Murofushi, T., 1999. Belowground carbon storage of Micronesian mangrove forests. Ecol. Res. 14, 409–413.

Furukawa, K., Wolanski, E., Mueller, H., 1997. Currents and sediment transport in mangrove forests. Estuar. Coast. Shelf Sci. 44, 301–310.

Gattuso, J.P., Frankignoulle, M., Wollast, R., 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. Annu. Rev. Ecol. Syst. 29, 405–434.

Giani, L., Bashan, Y., Holguin, G., Strangmann, A., 1996. Characteristics and methanogenesis of the Balandra lagoon mangrove soils, Baja California Sur. Mexico Geoderma 72, 149–160.

Giddins, R.L., Luscas, J.S., Neilson, M.J., Richards, G.N., 1986. Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae). Mar. Ecol. Prog. Ser. 33, 147–155.

Gillikin, D.P., De Wachter, B., Tack, J.F., 2004. Physiological response of two ecologically important Kenyan mangrove crabs exposed to altered salinity regimes. J. Exp. Mar. Biol. Ecol. 301, 93–109.

Giraldo Sánchez, B., 2005. Belowground productivity of mangrove forests in southwest Florida. Ph.D. thesis, Lousiana State University, 181 pp.

Hall, D., Lee, S.Y., Meziane, T., 2006. Fatty acids as trophic tracers in an experimental estuarine food chain: Tracer transfer. J. Exp. Mar. Biol. Ecol. 336, 42–53.

Hemminga, M.A., Slim, F.J., Kazungu, J., Ganssen, G.M., Nieuwenhuize, J., Kruyt, N.M., 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). Mar. Ecol. Prog. Ser. 106, 291–301.

Hernes, P.J., Benner, R., Cowie, G.L., Goni, M.A., Bergamaschi, B.A., Hedges, J.I., 2001. Tannin diagenesis in mangrove leaves from a tropical estuary: A novel molecular approach. Geochim. Cosmochim. Acta 65, 3109–3122.

Holmer, M., Kristensen, E., Banta, G., Hansen, K., Jensen, M.H., Bussawarit, N., 1994. Biogeochemical cycling of sulfur and iron in sediments of a south-east Asian mangrove, Phuket Island, Thailand. Biogeochemistry 26, 145–161.

Holmer, M., Anderson, F.Ø., Holmboe, N., Kristensen, E., Thongtham, N., 2001. Spatial and temporal variability in benthic processes along a mangrove-seagrass transect near the Bangrong Mangrove, Thailand. Wetlands Ecol. Manag. 9, 141–158.

Hsieh, H.L., Chen, C.P., Chen, Y.G., Yang, H.H., 2002. Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary: $\delta^{13}C$ and $\delta^{34}S$ signals. Mar. Ecol. Prog. Ser. 227, 145–155.

Jay, D.A., Musiak, J.D., 1994. Particle trapping in estuarine tidal flows. J. Geophys. Res. 99, 20445–20461.

Jennerjahn, T.C., Ittekkot, V., Carvalho, C.E.V., Ovalle, A.R.C., Rezende, C. E., Erlenkeuser, H., 1999. Temporal variability of amino acid, hexosamine and carbohydrate fluxes on the eastern Brazilian continental margin related to discharge of the São Francisco River, Brazil. In: Knoppers, B., Ekau, W. (eds.) JOPS-II: sedimentation process at East and Northeast Brazil Shelf. Geo.-Mar. Lett. 19, 202–208.

Jennerjahn, T.C., Ittekkot, V., 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. Naturwissenschaften 89, 23–30.

Jensen, M.M., Thamdrup, B., Rysgaard, S., Holmer, M., Fossing, H., 2003. Rates and regulation of microbial iron reduction in sediments of the Baltic-North Sea transition. Biogeochemistry 65, 295–317.

Kennedy, H., Gacia, E., Kennedy, D.P., Papadimitriou, S., Duarte, C.M., 2004. Organic carbon sources to SE Asian coastal sediments. Estuar. Coast. Shelf Sci. 60, 59–68.

Kieckbusch, D.K., Koch, M.S., Serafy, J.E., Anderson, W.T., 2004. Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. Bull. Mar. Sci. 74, 271–285.

Killops, S.D., Frewin, N.L., 1994. Triterpenoid diagenesis and cuticular preservation. Org. Geochem. 21, 1193–1209.

Kitheka, J.U., Ongwenyi, G.S., Mavuti, K.M., 2002. Dynamics of suspended sediment exchange and transport in a degraded mangrove creek in Kenya. Ambio 31, 580–587.

Koch, M.S., Madden, C.J., 2001. Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangroves. Mar. Ecol. Prog. Ser. 219, 109–119.

Koch, B.P., Rullkötter, J., Lara, R.J., 2003. Evaluation of triterpenols and sterols as organic matter biomarkers in a mangrove ecosystem in northern Brazil. Wetl. Ecol. Manag. 11, 257–263.

Koch, B.P., Harder, J., Lara, R.J., Kattner, G., 2005. The effect of selective microbial degradation on the composition of mangrove derived pentacyclic triterpenols in surface sediments. Org. Geochem. 36, 273–285.

Kreuzwieser, J., Buchholz, J., Rennenberg, H., 2003. Emisson of methane and nitrous oxide by Australian mangrove ecosystems. Plant Biol. 5, 423–431.

Kristensen, E., 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia 426, 1–24.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers, with emphasis on sediment processes. J. Sea Res., doi:10.1016/j.seares.2007.05.004, in press.

Kristensen, E., 2007. Carbon balance in mangrove sediments: the driving processes and their controls. In: Tateda, Y., Upstill-Goddard, R., Goreau, T., Alongi, D., Nose, A., Kristensen, E., Wattayakorn, G. (Eds.), Greenhouse Gas and Carbon Balances in Mangrove Coastal Ecosystems. Maruzen, Tokyo, pp. 61–78.

Kristensen, E., Suraswadi, P., 2002. Carbon, nitrogen and phosphorus dynamics in creek water of a Southeast Asian mangrove forest. Hydrobiologia 474, 197–211.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51, 1557–1571.

Kristensen, E., Devol, A.H., Ahmed, S.I., Saleem, M., 1992. Preliminary study of benthic metabolism and sulfate reduction in a mangrove swamp of the Indus Delta, Pakistan. Mar. Ecol. Prog. Ser. 90, 287–297.

Kristensen, E., King, G.M., Holmer, M., Banta, G.T., Jensen, M.H., Hansen, K., Bussarawit, N., 1994. Sulfate reduction, acetate turnover and carbon metabolism in sediments of the Ao-Nam-Bor mangrove, Phuket, Thailand. Mar. Ecol. Prog. Ser. 109, 245–255.

Kristensen, E., Jensen, M.H., Banta, G.T., Hansen, K., Holmer, M., King, G.M., 1998. Transformation and transport of inorganic nitrogen in sediments of a southeast Asian mangrove forest. Aquat. Microb. Ecol. 15, 165–175.

Kristensen, E., Andersen, F.Ø., Holmboe, N., Holmer, M., Thongtham, N., 2000. Carbon and nitrogen mineralization in sediments of the Bangrong mangrove area, Phuket, Thailand. Aquat. Microb. Ecol. 22, 199–213.

Kristensen, E., Pilgaard, R., 2001. The role of fecal pellet deposition by leaf-eating sesarmid crabs on mineralization processes in a mangrove sediment (Phuket, Thailand). In: Aller, J.Y., Woodin, S.A., Aller, R.C. (Eds.), Organism-Sediment Interactions. Univ. South Carolina Press, Columbia, pp. 369–384.

Laegdsgaard, P., Johnson, C., 2001. Why do juvenile fish utilise mangrove habitats? J. Exp. Mar. Biol. Ecol. 257, 229–253.

Lallier-Verges, E., Perrussel, B.P., Disnar, J.-R., Baltzer, F., 1998. Relationships between environmental conditions and the diagenetic evolution of organic matter derived from higher plants in a modern mangrove swamp system (Guadeloupe, French West Indies). Org. Geochem. 29, 1663–1686.

Lee, S.Y., 1995. Mangrove outwelling—a review. Hydrobiologia 295, 203–212.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Mar. Ecol. Prog. Ser. 159, 275–284.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshwater Res. 49, 335–343.

Li, M.S., Lee, S.Y., 1998. Carbon dynamics of Deep Bay, eastern Pearl River Estuary, China. I. A mass balance budget and implications for shorebird conservation. Mar. Ecol. Prog. Ser. 172, 73–87.

Lin, G.H., Banks, T., Sternberg, L.D.L.O., 1991. Variation in δ^{13}C values for the seagrass *Thalassia testudinum* and its relations to mangrove carbon. Aquat. Bot. 40, 333–341.

Marchand, C., Albéric, P., Lallier-Vergès, E., Baltzer, F., 2006. Distribution and characteristics of dissolved organic matter in mangrove sediments pore waters along the coastline of French Guiana. Biogeochemistry 81, 59–75.

Marchand, C., Baltzer, F., Lallier-Verges, E., Alberic, P., 2004. Pore-water chemistry in mangrove sediments: relationship with species composition and developmental stages (French Guiana). Mar. Geol. 208, 361–381.

Marchand, C., Lallier-Vergès, E., Baltzer, F., 2003. The composition of sedimentary organic matter in relation to the dynamic features of a mangrove-fringed coast in French Guiana. Estuar. Coast. Shelf Sci. 56, 119–130.

Marchand, C., Disnar, J.-R., Lallier-Verges, E., Lottier, N., 2005. Early diagenesis of carbohydrates and lignin in mangrove sediments subject to variable redox conditions (French Guiana). Geochim. Cosmochim. Acta 69, 131–142.

Matsui, N., 1998. Estimated stocks of organic carbon in mangrove roots and sediments in Hinchinbrook Channel, Australia. Mangroves Salt Marshes 2, 199–204.

Mazda, Y., Ikeda, Y., 2006. Behavior of the groundwater in a riverine-type mangrove forest. Wetl. Ecol. Manag. 14, 477–488.

McKee, K.L., Faulkner, P.L., 2000. Restoration of biogeochemical function in mangrove forests. Restor. Ecol. 8, 247–259.

Mead, R., Xu, Y., Chong, J., Jaffé, R., 2005. Sediment and soil organic matter source assessment as revealed by the molecular distribution and carbon composition of *n*-alkanes. Org. Geochem. 36, 363–370.

Meziane, T., Lee, S.Y., Mfilinge, P.L., Shin, P.K.S., Lam, M.H.W., Tsuchiya, M., 2007. Inter-specific and geographical variations in the fatty acid composition of mangrove leaves: implications for using fatty acids as a taxonomic tool and tracers of organic matter. Mar. Biol. 150, 1103–1113.

Mfilinge, P.L., Atta, N., Tsuchiya, M., 2002. Nutrient dynamics and leaf litter decomposition in a subtropical mangrove forest at Oura Bay, Okinawa, Japan. Trees 16, 172–180.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2003. Fatty acids in decomposing mangrove leaves: microbial activity, decay and nutritional quality. Mar. Ecol. Prog. Ser. 265, 97–105.

Mfilinge, P.L., Meziane, T., Bachok, Z., Tsuchiya, M., 2005. Total lipid and fatty acid classes in decomposing mangrove leaves of *Bruguiera gymnorrhiza* and *Kandelia candel*: significance with respect to lipid input. J. Oceanogr. 61, 613–622.

Micheli, F., 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. J. Exp. Mar. Biol. Ecol. 171, 165–186.

Middelburg, J.J., Nieuwenhuize, J., Slim, F.J., Ohowa, B., 1996. Sediment biogeochemistry in an East African mangrove forest (Gazi Bay, Kenya). Biogeochemistry 34, 133–155.

Middelburg, J.J., Nieuwenhuize, J., Lubberts, R.K., van de Plassche, O., 1997. Organic carbon isotope systematics of coastal marshes. Estuar. Coast. Shelf Sci. 45, 681–687.

Middleton, B.A., McKee, K.L., 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J. Ecol. 89, 818–828.

Moers, M.E.C., Baas, M., de Leeuw, J.W., Boon, J.J., Schenk, P.A., 1990. Occurrence and origin of carbohydrates in peat samples from a red mangrove environment as reflected by abundances of neutral monosaccharides. Geochim. Cosmochim. Acta 54, 2463–2472.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Neilson, M.J., Richards, G.N., 1989. Chemical composition of degrading mangrove leaf litter and changes produced after consumption by mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae). J. Chem. Ecol. 15, 1267–1283.

Nielsen, O.I., Kristensen, E., Macintosh, D.J., 2003. Impact of fiddler crabs (*Uca* spp.) on rates and pathways of benthic mineralization in deposited shrimp pond waste. J. Exp. Mar. Biol. Ecol. 289, 59–81.

Newell, S.Y., 1996. Established and potential impacts of eukaryotic mycelial decomposers in marine/terrestrial ecotones. J. Exp. Mar. Biol. Ecol. 200, 187–206.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuar. Coast. Shelf Sci. 67, 239–250.

Odum, E.P., 1968. A research challenge: evaluating the productivity of coastal and estuarine water. In: Proceedings of the Second Sea Grant Conference, October. Univ. of Rhode Island, pp. 63–64.

Odum, E.P., Heald, E.J., 1975. The detritus based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), Estuarine Research. Academic Press, New York, pp. 265–286.

Oku, H., Baba, S., Koga, H., Takara, K., Iwasaki, H., 2003. Lipid composition of mangrove and its relevance to salt tolerance. J. Plant Res. 116, 37–45.

Ólafsson, E., Buchmayer, S., Skov, W.M., 2002. The east African decapod crab *Neosarmatium meinerti* (de Man) sweeps mangrove floors clean of leaf litter. Ambio 31, 569–573.

Opsahl, S., Benner, R., 1995. Early diagenesis of vascular plant tissues: lignin and cutin decomposition and biogeochemical implications. Geochim. Cosmochim. Acta 59, 4889–4904.

Opsahl, S., Benner, R., 1999. Characterization of carbohydrates during early diagenesis of five vascular plant tissues. Org. Geochem. 30, 83–94.

Poovachiranon, S., Tantichodok, P., 1991. The role of sesarmid crabs in the mineralization of leaf litter of *Rhizophora apiculata* in a mangrove, Southern Thailand. Res. Bull. Phuket Mar. Biol. Centre 56, 63–74.

Purvaja, R., Ramesh, R., 2001. Natural and anthropogenic methane emission from wetlands of south India. Environ. Manag. 27, 547–557.

Ridd, P.V., 1996. Flow through animal burrows in mangrove creeks. Estuar. Coast. Shelf Sci. 43, 617–625.

Rafii, Z.A., Dodd, R.S., Fromard, F., 1996. Biogeographic variation in foliar waxes of mangrove species. Biochem. System Ecol. 24, 341–345.

Robertson, A.I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. J. Exp. Mar. Biol. Ecol. 102, 237–248.

Robertson, A.I., 1988. The decomposition of mangrove leaf litter in tropical Australia. J. Exp. Mar. Biol. Ecol. 116, 235–247.

Robertson, A.I., Alongi, D.M., Boto, K.G., 1992. Food chains and carbon fluxes. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems, Coastal and Estuarine Series 41. American Geophysical Union, Washington DC, USA, pp. 293–326.

Robertson, A.I., Blaber, S.J.M., 1992. Plankton, epibenthos and fish communities. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 173–224.

Rönnbäck, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol. Econ. 29, 235–252.

Rönnbäck, P., Troell, M., Zetterström, T., Babu, D.E., 2003. Mangrove dependence and socio-economic concerns in shrimp hatcheries of Andhra Pradesh, India. Environ. Conserv. 30, 344–352.

Sasekumar, A., 1974. Distribution of mangrove fauna on a Malayan mangrove shore. J. Anim. Ecol. 43, 51–64.

Sassen, R., 1977. Early diagenesis of fatty acids in mangrove peats, St Croix, U.S. Virgin Island. In: Interdisciplinary Studies of Peat and Coal Origins, Geological Society of America Microform Publication, N° 7.

Schories, D., Barletta-Bergan, A., Barletta, M., Krumme, U., Mehlig, U., Rademaker, V., 2003. The keystone role of leaf-removing crabs in mangrove forests of North Brazil. Wetl. Ecol. Manag. 11, 243–255.

Schrijvers, J., Camargo, M.G., Pratiwi, R., Vincx, M., 1998. The infaunal macrobenthos under East African *Ceriops tagal* mangroves impacted by epibenthos. J. Exp. Mar. Biol. Ecol. 222, 175–193.

Schwamborn, R., Voss, M., Ekau, W., Saint-Paul, U., 1999. Stable isotope composition of particulate organic matter and zooplankton in North-East Brazilian shelf waters. Arch. Fish. Mar. Res. 47, 201–210.

Sheaves, M., Molony, B., 2000. Short-circuit in the mangrove food chain. Mar. Ecol. Prog. Ser. 199, 97–109.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131, 1–7.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannick, N.T., Cocheret de la Morinière, E., van der Velde, G., 1997. Leaf litter removal by the snail *Terebralia palustris* (Linneaus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenia). J. Exp. Mar Biol. Ecol. 215, 35–48.

Spitzy, A., Leenheer, J., 1991. Dissolved organic carbon in rivers. In: Degens, E.T., Kempe, S., Richey, J.E. (Eds.), Biogeochemistry of major world rivers Scope 42. Wiley, U.K., pp. 214–232.

Susilo, A., Ridd, P.V., Thomas, S., 2005. Comparison between tidally driven groundwater flow and flushing of animal burrows in tropical mangrove swamps. Wetl. Ecol. Manag. 13, 377–388.

Tam, N.F.Y., Wong, Y.S., 1993. Retention of nutrients and heavy-metals in mangrove sediments receiving waste-water of different strengths. Environ. Technol. 14, 719–729.

Tam, N.F.Y., Wong, Y.S., Lan, C.Y., Wang, L.N., 1998. Litter production and decomposition in a subtropical mangrove swamp receiving wastewater. J. Exp. Mar. Biol. Ecol. 226, 1–18.

Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neoepisesarma versicolor*) offered different food sources. Estuar. Coast. Shelf Sci. 65, 213–222.

Tremblay, L., Benner, R., 2006. Microbial contributions to N-immobilization and organic matter preservation in decaying plant detritus. Geochim. Cosmochim. Acta 70, 133–146.

Twilley, R.R., 1985. The exchange of organic carbon in basin mangrove forests in a southwestern Florida estuary. Estuar. Coast. Shelf Sci. 20, 543–557.

Twilley, R.R., Ejdung, G., Romare, P., Kemp, W.M., 1986. A comparative study of decomposition, oxygen consumption and nutrient release for selected aquatic plants occurring in an estuarine environment. Oikos 47, 190–198.

Twilley, R.R., Chen, R.H., Hargis, T., 1992. Carbon sinks in mangrove forests and their implications to the carbon budget of tropical coastal ecosystems. Water Air Soil Pollut. 64, 265–288.

Twilley, R.R., Poro, M., Garcia, V.H., Rivera-Monroy, V.H., Zambrano, R., Bodero, A., 1997. Litter dynamics in riverine mangrove forests in the Guayas River Estuary. Ecuador. Oecologia 111, 109–122.

Valiela, I., Bowen, J.L., York, J.K., 2001. Mangrove forests: one of the world's threatened major tropical environments. Bioscience 51, 807–815.

Versteegh, G.J.M., Schefuß, E., Dupont, L., Marret, F., Sinninghe-Damst'e, J.S., Jansen, J.H.F., 2004. Taraxerol and *Rhizophora* pollen as proxies for tracking pas mangrove ecosystem. Geochim. Cosmochim. Acta 68, 411–422.

Victor, S., Golbuu, Y., Wolanski, E., Richmond, R.H., 2004. Fine sediment trapping in two mangrove-fringed estuaries exposed to contrasting land-use intensity, Palau, Micronesia. Wetl. Ecol. Manag. 12, 277–283.

Wafar, S., Untawale, A.G., Wafar, M., 1997. Litter fall and energy flux in a mangrove ecosystem. Estuar. Coast. Shelf Sci. 44, 111–124.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Webb, A.P., Eyre, B.D., 2004. The effect of natural populations of the burrowing and grazing soldier crab (*Mictyris longicarpus*) on sediment irrigation, benthic metabolism and nitrogen fluxes. J. Exp. Mar. Biol. Ecol. 309, 1–19.

Wells, F.E., 1984. Comparative distribution of macromolluscs and macrocrustaceans in a North-western Australian mangrove system. Aust. J. Mar. Freshw. Res. 35, 591–596.

Wolanski, E., 1995. Transport of sediment in mangrove swamps. Hydrobiologia 295, 31–42.

Woodroffe, C.D., 1992. Mangrove sediments and geomorphology. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical mangrove ecosystems. (Coastal and estuarine studies 41) AGU, Washington, pp. 7–41.

Wooller, M., Smallwood, B., Jacobson, M., Fogel, M., 2003. Carbon and nitrogen stable isotopic variation in *Laguncularia racemosa* (L.) (white mangrove) from Florida and Belize: implications for trophic level studies. Hydrobiologia 499, 13–23.

Zieman, J.C., Macko, S.A., Mills, A.L., 1984. Role of seagrasses and mangroves in estuarine foodwebs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. Bull. Mar. Sci. 35, 380–392.

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Review

Ethnobiology, socio-economics and management of mangrove forests: A review

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ABSTRACT

There is growing research interest in the ethnobiology, socio-economics and management of mangrove forests. Coastal residents who use mangroves and their resources may have considerable botanical and ecological knowledgeable about these forests. A wide variety of forest products are harvested in mangroves, especially wood for fuel and construction, tannins and medicines. Although there are exceptions, mangrove forest products are typically harvested in a small-scale and selective manner, with harvesting efforts and impacts concentrated in stands that are closer to settlements and easiest to access (by land or by sea). Mangroves support diverse, local fisheries, and also provide critical nursery habitat and marine productivity which support wider commercial fisheries. These forests also provide valuable ecosystem services that benefit coastal communities, including coastal land stabilization and storm protection. The overlapping of marine and terrestrial resources in mangroves creates tenure ambiguities that complicate management and may induce conflict between competing interests. Mangroves have been cut and cleared extensively to make way for brackish water aquaculture and infrastructure development. More attention is now given to managing remaining forests sustainably and to restoring those degraded from past use. Recent advances in remotely sensed, geo-spatial monitoring provide opportunities for researchers and planners to better understand and improve the management of these unique forested wetlands.

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1. Introduction

Mangroves have been extensively studied for decades by botanists, ecologists and marine scientists (Macnae, 1968; Chapman, 1976; Saenger et al., 1983; Tomlinson, 1986; Kathiresan and Bingham, 2001; Lacerda, 2002). Yet, it was not until the 1980s and early 1990s that significant research attention was brought to bear on the human interactions with these unique forested wetlands (FAO, 1985; Hamilton et al., 1989; FAO, 1994; Cormier-Salem, 1999). Earlier works were mostly descriptive, documenting the status and uses of mangroves by coastal communities (e.g., Walsh, 1977; Taylor, 1982; Christensen, 1982; Kunstadter et al., 1986; Field and Dartnall, 1987; Diop, 1993; Lacerda, 1993). By contrast, recent research on mangroves is more analytical, examining humans as ecological agents of disturbance and change in mangrove ecosystems. These studies have applied a mix of ecological, economic, ethnographic, historical and geo-spatial methods to quantify the diverse values of mangrove forests and to probe cause–effect relationships between people and mangroves in a variety of geographic, cultural and political-economic contexts (e.g., Dewalt et al., 1996; Ellison and Farnsworth, 1996; Ewel et al., 1998b; Rönnbäck, 1999; Vandergeest et al., 1999; Kovacs, 2000; Barnes, 2001; Walters, 2003, 2005b; Dahdouh-Guebas et al., 2006a; Lopez-Hoffman et al., 2006).

This review paper synthesizes research on the ethnobiology, socio-economics and management of mangrove forests, and also includes a brief review of geo-spatial monitoring tools as these have been applied to study mangroves. These topics span an enormously diverse range of literature. As such, different subtopics are necessarily dealt with succinctly. An attempt was made to include the most significant publications as well as a good number of the less noted, but also important research works. The extensive bibliography can serve as a resource for readers interested in further exploration of the subject.

Population pressure is typically greatest along the coast, so it is little surprise that human influences on the world's mangrove forests are significant and growing. Mangroves have been cleared and degraded on an alarming scale during the past four decades (Valiela et al., 2001; Wilkie and Fortuna, 2003; Duke et al., 2007), yet they remain an important source of wood and food products and provide vitally important environmental services for coastal communities throughout the tropics (Balmford et al., 2002). These values still receive relatively little attention or recognition from government policy-makers and the development community, and the myriad influences people have on these forests continue to be overlooked by many mangrove researchers. It is hoped that this review paper will provide some corrective to this neglect.

2. Ethnobiology of mangroves

Local ecological knowledge (LEK) or traditional ecological knowledge (TEK) are closely related concepts that are broadly inclusive of many different types of ecologically relevant knowledge, ranging from traditional use of specific plants and animals and essential knowledge critical to harvesting natural resources, through complex understandings of the functioning of local ecosystems, to cultural beliefs and religious views of human–environment relations (Berkes, 1999; Davis and Wagner, 2003).

There is an implicit assumption that most LEK is accumulated through experiences of close contact with the natural environment, and therefore locality plays a large part in shaping this knowledge (Davis and Wagner, 2003). The local scale has also been shown to be important in resource extraction patterns and resulting impacts on mangroves (Tomlinson, 1986; Ewel et al., 1998b; Kovacs, 1999; Dahdouh-Guebas et al., 2000a, 2000b, 2006a; Walters, 2005a, 2005b; Lopez-Hoffman et al., 2006). The role of LEK in shaping resource use in mangroves is therefore of great interest for management of these ecosystems. There is much opportunity to integrate indigenous knowledge into contemporary frameworks for conservation and sustainable management, or in a *priori* understanding of forest dynamics and local dependency using ethnoscientific approaches (Rist and Dahdouh-Guebas, 2006) and modeling (Berger et al., 2008). Studies of mangrove LEK and ethnobiology can be split into two general categories: one focusing on the functioning of the ecosystem, including knowledge of ecological processes and how different ecological components interact with each other; the other focusing more on specific species or taxa and their use for anthropocentric purposes, often termed ethnotaxonomy or ethnobotany (Berlin, 1973).

Studies in Mexico, the Philippines, Tanzania, Kenya, India and Venezuela are worth briefly describing as examples where LEK representing basic ecosystem dynamics has been documented. Kovacs (2000) showed how Mexican fishermen have extensive knowledge of mangrove system dynamics, including previously undocumented sources of local environmental disturbance that help explain changes in the forest over time. Similarly, Walters (2003, 2005b) sought the knowledge of local fishermen and coastal residents in the Philippines to assist in mapping and explaining changes to the distribution of mangrove forests. Tobisson et al. (1998) found intricate LEK within Zanzibar fishing communities relating to tidal patterns and currents, but linked to mangroves and associated fisheries. In Kenya, Crona (2006) similarly showed a large body of LEK related to complex ecological linkages between mangroves and the surrounding seascape, and noted marked differences in local peoples' knowledge based on their gear types and modes of resource extraction from the mangrove. This heterogeneous distribution of LEK between user groups is a common theme throughout much LEK work on mangroves and other systems (Kovacs, 2000; Dahdouh-Guebas et al., 2000b; Ghimire et al., 2004; Vayda et al., 2004; Walters, 2004; Hernández Cornejo et al., 2005; Dahdouh-Guebas et al., 2006a). The benefit of such heterogeneity and spatially distributed LEK is that it can be valuable for documenting and understanding variations in patterns of mangrove use and change that would otherwise not be apparent with larger-scale scientific assessments and monitoring (Kovacs, 2000).

Understanding of ecosystem dynamics by local communities has also proven valuable as a background to reconstruct historical use and impact on mangroves (Walters, 2003; Dahdouh-Guebas et al., 2004, 2005b), although efforts should be made to validate such information before it is applied to policy and management decisions (Kovacs, 2000; Hernández Cornejo et al., 2005). Validation, in this sense, means sound interpretation by cross-checking statements with other information sources, including pre-existing historical documents, data from remotely sensed imagery and modeling, and experimental field-testing (Kovacs et al., 2001a, b; Vayda et al., 2004; Hernández Cornejo et al., 2005; Bart, 2006; Lopez-Hoffman et al., 2006). This historical aspect of LEK can, when used in conjunction with scientific results, also increase the chance of including important ecological information potentially missed by short-term duration scientific studies (Moller and Berkes, 2004; Bart, 2006). Examples of this can be seen in findings on the role of caterpillars and hurricanes as agents of mangrove forest disturbance in Mexico (Kovacs, 2000), and in information on sea urchin infestations in Kenya (Crona, 2006).

The second knowledge category is represented by ethnobotany which relates to taxonomy and use of specific plants for different purposes. This is a better-documented field than the LEK of system dynamics reviewed above, although very fragmentary from a global perspective. In many coastal communities, mangrove dependence is high and both wood and non-wood products are used for a multitude of purposes. Discussions of LEK as this pertains to mangrove resource use are embedded in subsequent sections of the paper that detail forest and aquatic resource uses. Nonetheless, a few general comments and examples are warranted here.

Like the aforementioned studies on knowledge of basic ecology, LEK that is related to mangrove resource use is often well developed, but heterogeneous between and within coastal communities in ways that typically reflect their varied experience and dependence on the use of particular resources. For example, Lopez-Hoffman et al. (2006) found sharp differences in the perceptions and practices of older, more experienced versus younger, less experienced mangrove wood harvesters in Venezuela. The same is true for Kenyan mangrove users, as those with greater experience were better able than others to identify forest vegetation decline (Dahdouh-Guebas et al., 2000b). Similarly, studies of coastal residents in the Philippines who were engaged in the local silviculture of mangrove trees revealed that knowledge among planters about propagation and management was considerable, but varied enormously depending on personal experience and opportunities to learn from others more knowledgeable. The differences in knowledge had significant consequences for the relative success of individual mangrove tree planters (Vayda et al., 2004; Walters, 2004).

However, as knowledgeable as local people were sometimes found to be, it is notable that mangrove users in the aforementioned Venezuelan and Philippine cases were sometimes found to act in ways that were inconsistent with their knowledge and avowed beliefs by, for example, over-cutting and clearing mangroves that they otherwise viewed as important to protect (Vayda and Walters, 1999; Walters, 2004; Lopez-Hoffman et al., 2006). This gap between knowledge and behavior, also known as 'cognitive dissonance' (Festinger, 1957), is displayed by most humans to various degrees and is often caused by conflicting interests or incentives. While this does not invalidate the LEK per se, such knowledge should not be assumed to always guide the behavior of local users in terms of resource use, etc. (Vayda et al., 2004; Bart, 2006). Economic incentives, property rights and participation in the management process are also likely to influence such behavior.

3. Mangrove forest products: use and consequences

3.1. Mangrove forest users and uses

Non-timber forest products are recognized as important economic resources, particularly to rural, marginalized communities (Vedeld et al., 2004). Many coastal communities in the tropics are characterized by relative geographic isolation, chronic poverty and significant dependence on the harvest of marine and coastal resources for their livelihood (Kunstadter et al., 1986). The majority of people living in or near mangrove areas derive their principal income from fishing and related activities. The direct harvest of mangrove wood and plants is rarely a full-time occupation for them, but a great many rely on these products to meet subsistence needs for fuel and construction materials, and for others the harvest and sale of mangrove forest products is an important income supplement (Christensen, 1982; FAO, 1985, 1994; Kunstadter et al., 1986; Diop, 1993; Lacerda et al., 1993; Spalding et al., 1997; Glaser, 2003; Walters, 2005a; Lopez-Hoffman et al., 2006; Rönnbäck et al., 2007a).

The two most widespread uses of mangrove wood are for fuel and construction. Many common mangrove tree species, e.g., *Rhizophora* species produce wood that is dense, hard and often rich in tannins (FAO, 1994; Bandaranayake, 1998). Such wood burns long and hot, and so is highly attractive for making charcoal or consuming directly as firewood (Brown and Fischer, 1918; Chapman, 1976; Christensen, 1982, 1983b; Taylor, 1982; Bhattacharyya, 1990; Ewel et al., 1998a; Walters, 2005a; Dahdouh-Guebas et al., 2006a). The harvest of mangrove for fuelwood is widespread throughout the coastal tropics (Fig. 1A and D). In some countries, mangrove wood historically formed an important commercial fuel for industries like bakeries and clay-firing kilns, although this is less common today because of the ready availability of alternative fuels, like natural gas and electricity, and policies aimed at discouraging mangrove cutting (Lacerda et al., 1993; Naylor et al., 2002; Walters, 2003). Nonetheless, remote coastal communities in many parts of the tropics continue to depend heavily on mangrove wood for domestic fuelwood consumption, and commercial markets that sell mangrove charcoal to nearby towns and urban centers are not uncommon (Untawale, 1987; Walters and Burt, 1991; Alvarez-Leon, 1993; Allen et al., 2000; Dahdouh-Guebas et al., 2000b; Glaser, 2003).

The qualities of strength and durability (including pest- and rot-resistance) also make mangrove wood well-suited for use in construction (Adegbehin, 1993; Bandaranayake, 1998; Kairo et al., 2002; Walters, 2005a). Yet, the typically short and contorted growth form of tree stems of common genera such as *Avicennia* and *Sonneratia* renders them of limited value for large, commercial-sized lumber. The extraction of construction wood from mangroves is thus limited mostly to domestic consumption and sale of small-size posts to targeted local and regional markets (Fig. 1C). Mangrove wood is widely used in coastal communities for residential construction (posts, beams, roofing, fencing) and to make fish traps/weirs (Adegbehin, 1993; Alvarez-Leon, 1993; Rasolofo, 1997; Ewel et al., 1998a; Semesi, 1998; Kovacs, 1999; Primavera et al., 2004; Walters, 2004). Fronds from the mangrove "nipa" palm (*Nypa fruticans* (Thunb.) Wurmb.) are particularly valued in Southeast Asia for use in roofing and as thatch in walls and floor mats (Aksornkoae et al., 1986; Fong, 1992; Basit, 1995; Spalding et al., 1997; Walters, 2005a). Mangrove wood is also used in some countries for building boats, furniture, wharf pilings, telegraph poles, construction scaffolding, railway girders and mine timbers (Walsh, 1977; Mainoya et al., 1986; Adegbehin, 1993; Bandaranayake, 1998; Primavera et al., 2004; Lopez-Hoffman et al., 2006).

In addition to wood for fuel and construction, mangrove forest trees are also widely valued for their bark (used in tanning and dyes)

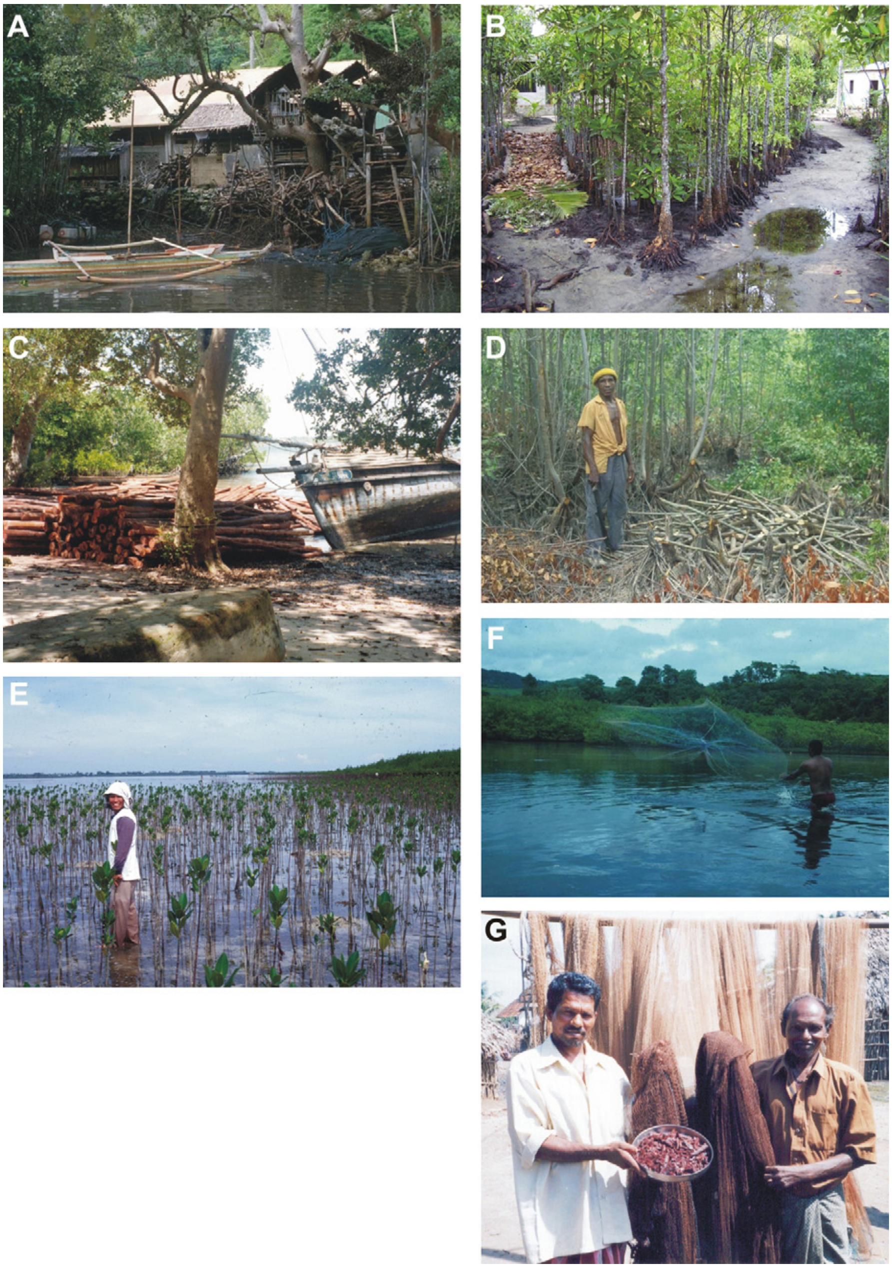

Fig. 1. (A) Fishermen in Bais Bay, Philippines commonly build their homes adjacent to mangroves where they gain ready access to wood products and favored fishing spots, and benefit from the storm protective value of mangrove trees. (B) An illustration of the concept of living in mangroves in Balapitiya, Sri Lanka: houses were built within a mangrove and ***Bruguiera gymnorrhiza*** assemblages were cut in such a way that they form access paths to each house. (C) Mangrove poles at the Sita landing place in Mida Creek, Kenya waiting to be transported to markets and hardware stores. (D) Mangroves in Mankote, Saint Lucia are often cut to make charcoal, a fuel preferred by many West Indians for barbecuing. (E) Gleaners like this woman on Banacon Island, Philippines are free to harvest for shellfish within a plantation of ***Rhizophora stylosa*** as long as they do not disturb the young trees. (F) Simple fishing techniques like this throw-net are effective for capturing fish in the murky, brackish waters of the Mankote mangrove, Saint Lucia. (G) Fishermen holding a tray with pieces of ***Ceriops decandra*** bark used for dyeing fishing nets near Kakinada in Andhra Pradesh, India. They also show two freshly dyed nets and in the background previously dyed nets are hung to dry. Adopted from Dahdouh-Guebas (2006). (***Note***: photos in Fig. 1A and D–F by Brad Walters; (B), (C) and (G) by Farid Dahdouh-Guebas).

and wood fiber (to make rayon and paper); as sources of animal fodder, vegetable foods, and diverse traditional medicines and toxicants (see Bandaranayake, 1998, 2002 for a reviews); and as habitats for honey bees and hunted wildlife (see Table 1; Fig. 1G).

3.2. *Patterns and consequences of forest use*

Different mangrove species have different wood properties, making some more suitable than others for specific uses (FAO, 1994). For example, trees from the Rhizophoraceae family (*Rhizophora*, *Ceriops*, *Bruguiera*) are characterized by hard, dense wood that is rich in tannins and, as such, is widely valued for construction, fuelwood and tannin extraction, yet this wood is not suitable for lumber or furniture-making because of its tendency to split (Ewel et al., 1998a). Studies have documented mangrove wood harvesting that is size- and species-selective, and harvesters willing to venture widely in search of particular trees that are used in construction and have high local market value (Rasolofo, 1997; Dahdouh-Guebas et al., 2000b; Hauff et al., 2006).

However, despite differences in wood character and quality, research suggests that mangrove wood users are often flexible in their preferences, and willing to substitute favored mangrove

Table 1
Summary of mangrove forest products and uses, with selected published references

Forest products and use	Selected references
Wood for fuel (charcoal, firewood)	See text
Wood for construction materials	See text
Tree bark for tannins, dyes	Chapman, 1976; Aksornkoae et al., 1986; Mainoya et al., 1986; Lacerda et al., 1993; Dahdouh-Guebas et al., 2000b; Primavera and de la Pena, 2000; Glaser, 2003
Wood fiber for rayon, paper	Christensen, 1982; FAO, 1985; Bhattacharyya, 1990; Ong, 1995; Bandaranayake, 1998; Ewel et al., 1998a
Buds and leaves for vegetables, alcohol, livestock fodder	Morton, 1965; Walsh, 1977; Christensen, 1983b; Semesi, 1998; Dahdouh-Guebas et al., 2006a; Jayatissa et al., 2006
Plant parts and extracts for medicines, pesticides	Sangdee, 1986; Chang and Peng, 1987; Bandaranayake, 1998, 2002; Sánchez et al., 2001; Primavera et al., 2004
Habitat for collecting honey, bees wax, and hunting wildlife	Hamilton and Snedaker, 1984; Untawale, 1987; Adegbehin, 1993; FAO, 1994; Basit, 1995; Sathirathai and Barbier, 2001; Nagelkerken et al., 2008

species for less favored ones – or even non-mangrove species – especially where the preferred wood has become less available or too costly to obtain (Walters, 2003). Harvest for fuelwood is often non-selective: some species are clearly better than others, especially for making charcoal, but evidence suggests people will harvest and burn as fuelwood almost any type of mangrove tree and are more likely to make decisions about which ones to harvest based on relative availability, rather than species preference (Walters, 2005a). In short, the material poverty of coastal communities and their widespread dependence on mangrove wood products to meet basic subsistence needs means users are often not in a good position to be selective and, instead, will harvest what is most readily available to them (Ewel et al., 1998a).

Patterns of harvest reflect the spatial distribution and relative accessibility of mangroves, which varies depending on local geomorphology and hydrology, socio-economic conditions, and past human disturbance (Ewel et al., 1998a; Hauff et al., 2006; Walters, 2003). Small-block clear-felling is applied, but to a limited extent and usually only in intensively managed forests (Hussain, 1995; Walters, 2004). Individual tree species vary dramatically in natural distribution within a mangrove and are often clumped in mono-specific stands. The dense above-ground root and branch growth of mangroves tends to make access to and clearing of forests difficult. These factors encourage the selective cutting of individual tree stems, branches and roots. To avoid such difficulties, pond construction in mangroves often starts with dike enclosures to retain water and kill the trees by flooding (for later clear-felling). It is also common for wood harvesting to concentrate on either the landward or seaward edges of a forest or along mangrove creeks, sites more readily accessible by foot during low tide or by boat during high tide (Walters, 2005a; Hauff et al., 2006; Lopez-Hoffman et al., 2006). Other things being equal, mangroves in proximity to human settlements are more likely to be heavily harvested. But whether and where mangroves are cut can also reflect the actions of government and coastal land owners who may restrict forest cutting. Yet, such restrictions may have limited effect on actual cutting practices given the practical difficulties of monitoring sites that are remote and simultaneously accessible by land and sea (Dahdouh-Guebas et al., 2000b, 2006a; Glaser, 2003; Walters, 2003, 2005a; Lopez-Hoffman et al., 2006).

Considerable research has been devoted to understanding the ecological effects of selection cutting and clear-felling as these treatments are applied in certain managed forests in Ecuador and South and Southeast Asia (Christensen, 1983a; FAO, 1985; Putz and Chan, 1986; Azariah et al., 1992; FAO, 1994; Nurkin, 1994; Blanchard and Prado, 1995; Hussain, 1995; Gong and Ong, 1995). But the relevance of this work is limited given that relatively little of the world's mangroves are subject to this kind of intensive forest management. In contrast, there has been remarkably little study of the ecological effects of informal, small-scale mangrove cutting by local coastal communities, a commonplace phenomenon that impacts mangroves in almost every region of the world.

Initial studies suggest that small-scale cutting typically involves the selective removal of one or few tree stems and/or branches at a time, causing localized structural disturbances that create relatively small gaps in the forest canopy (Smith and Berkes, 1993; Ewel et al., 1998b; Allen et al., 2001; Pinzon et al., 2003; Walters, 2005b). The creation of such gaps can alter micro-environmental conditions within the forest (Ewel et al., 1998b). Whereas clear-felling of mangroves tends to encourage regeneration of tree species that are better able to exploit large openings through seed dispersal and establishment, such as *Rhizophora* spp. and *Bruguiera* spp. (Putz and Chan, 1986; Blanchard and Prado, 1995; Hussain, 1995; Kairo et al., 2002; but see Azariah et al., 1992), the smaller openings created by selective cutting may better favor regeneration of species that successfully re-sprout/coppice from surviving stems, including *Sonneratia* spp., *Avicennia* spp., and *Laguncularia racemosa* (L.) Gaertn. f. (Smith and Berkes, 1993; Walters, 2005b; but see Pinzon et al., 2003). In contrast, the adult trees of *Rhizophora*, *Ceriops* and other genera of the Rhizophoraceae lack reserve meristems (Tomlinson, 1986), and therefore require replacement by new seedlings.

The cumulative effects of such selective cutting on a forest include reduced adult tree density, canopy height and canopy closure (Walters, 2005b; Hauff et al., 2006; Lopez-Hoffman et al., 2006). Heavily impacted stands are often characterized by few species of widely dispersed, dwarf-like trees manifesting a distinctly "bushy" appearance. Collateral damage from selective wood cutting may result in a net increase of dead wood in the forest (Allen et al., 2000). By contrast, local people in some settings intentionally forage for deadwood (for fuel) and thereby reduce levels of naturally-occurring deadwood (Walters, 2005a). These various changes in forest structure, composition and micro-climate can significantly alter the habitat conditions for establishment of seedlings (Bosire et al., 2003, 2006) and for resident marine and terrestrial animals (e.g., Barnes, 2001; Bosire et al., 2004, 2005a, b; Crona and Rönnbäck, 2005; Crona et al., 2006; Crona and Rönnbäck, 2007).

4. Mangrove-associated fisheries

4.1. Mangrove support functions to fisheries

Fishery species that use mangroves as habitat can be classified into permanent residents, spending their entire life cycle in mangrove systems, temporary long-term residents, associated with mangroves during at least one stage in their life cycle, and temporary short-term residents or sporadic users of the mangrove habitat (Robertson and Duke, 1990b). The critical early life stages, i.e. the larvae and juveniles, of many fish and shellfish species utilize mangroves as nursery grounds, whereafter they emigrate to other systems such as coral reefs as adults (Matthes and Kapetsky, 1988; Robertson and Duke, 1990a; Ogden, 1997; Barletta-Bergan et al., 2002a, b; Nagelkerken et al., 2002; Crona and Rönnbäck, 2007; Serafy and Araújo, 2007). Through the abundance of early life stages, mangroves also attract carnivorous fishes that conduct feeding migrations to mangrove areas.

The postlarvae of many commercial penaeid shrimps enter mangrove-dominated environments, where they develop into juveniles and subadults before migrating back to sea to complete their life cycle (e.g., Dall et al., 1990; Chong et al., 1990, 1996; Vance et al., 1996; Primavera, 1998b; Rönnbäck et al., 1999, 2002). Mangrove mud crabs, sergestid shrimps, and giant freshwater prawn are other crustaceans of commercial value that utilize mangroves as habitat during some life stage. Highly valued food and game fish that have a close association with mangroves include groupers, snappers, sea-perch, mullets, catfishes, milkfish, and tarpons. Mangroves also support many mollusk species that constitute an important in situ fishery. Edible species of oysters, mussels, cockles, and gastropods are collected extensively for local consumption, usually by the families of local fishermen, and/or market sale, e.g., the mangrove clam *Anodontia edentula* Linn. (Primavera et al., 2002). For more detailed information on fish and invertebrates associated with mangrove environments see Macintosh (1982), Rönnbäck (1999), and the biogeographic analysis by Matthes and Kapetsky (1988).

Mangroves also indirectly support fisheries where the harvested species never enter mangrove environments. Mangroves, seagrass beds, unvegetated shallows, and coral reefs can exist in isolation from each other, but commonly form integrated ecosystems of high productivity (Yanez-Arancibia et al., 1993; Ogden, 1997; Rönnbäck, 1999). For example, the ability of mangroves to control water quality (trapping and assimilating sediment and nutrients) is a prerequisite for coral reef functioning, including fisheries production (Kühlmann, 1988).

Another indirect support function to fisheries is the bioeconomics of shrimp trawling. Penaeid shrimps, which dominate global shrimp catches, are one of the most important fishery resources worldwide in terms of volume of catch and value per unit catch (Dall et al., 1990). Because penaeid shrimp sales generate most of the revenues from mechanized trawling in developing countries, shrimps (and indirectly their nursery habitat, i.e. mangroves) effectively subsidize commercial fish harvesting efforts by these vessels, including fish species not using mangroves as habitat (Turner, 1977; Bennett and Reynolds, 1993; Rönnbäck, 1999). Trawl catch ratio between marketed fish and penaeids in Indonesia was 667 kg of fish for every 100 kg of shrimps trawled (Turner, 1977).

Apart from fisheries aimed directly for human consumption, mangroves also support aquaculture operations by providing seed, broodstock and feed inputs (Rönnbäck, 1999; Naylor et al., 2000). Mangroves function as nursery grounds for the early life stages of aquaculture species like penaeid shrimps, mangrove mudcrabs, sea-perch, snapper, grouper, milkfish, etc. (Matthes and Kapetsky, 1988; Bagarinao, 1994; Primavera, 1998b; Walton et al., 2006a; Cannicci et al., 2008; Nagelkerken et al., 2008). The collection of wild seed, which supports major fishery operations in many countries, has however been criticized for bycatch problems. For example, the tiger prawn (*Penaeus monodon* Fabricius), which dominates shrimp aquaculture production, constitutes a very small proportion (down to 0.1%) of fish and invertebrate larvae in seed collector's catch (reviewed by Primavera, 1998a). This bycatch is usually sorted out on land and not returned to the sea, which could have significant negative impacts on biodiversity and capture fisheries production in the area. Some countries have developed hatcheries for seed production of cultured species. This may have reduced the dependence on mangroves to produce wild seed, but has increased demand for wild-caught broodstock instead. For instance, penaeid shrimp hatcheries often rely on the continuous input of mature females to sustain productivity as well as to avoid inbreeding problems. The mangroves in the Godavari delta, India, have been estimated to support an annual catch around 50,000 tiger prawn (*Penaeus monodon*) spawners, valued at US$ 6 million (Rönnbäck et al., 2003).

Mangroves and aquaculture are not necessarily incompatible. Already, the culture of seaweeds, mollusks and fish in cages in subtidal waterways is both compatible with mangroves and amenable to small-scale, family-level operations (Primavera, 1993, 1995). But there remains a need for mangrove-friendly aquaculture technology in the intertidal forest or swamp that does not require clearing of the trees. Development of such technology is on two levels: (a) silvofisheries or aquasilviculture where the low-density culture of crabs and fish is integrated with mangroves and (b) mangrove filters where adjacent mangrove stands are used to absorb effluents from high-density shrimp and fish culture ponds (Primavera, 2000b; Primavera et al., 2007). Present-day versions of integrated forestry–fisheries–aquaculture can be found in the traditional *gei wai* ponds in Hong Kong, mangrove–shrimp ponds in Vietnam, aquasilviculture in the Philippines, and silvofisheries in Indonesia (Primavera, 2000b). The Southeast Asian Fisheries Development Center Aquaculture Department has recently put out guidelines for sustainable aquaculture in mangrove ecosystems (Bagarinao and Primavera, 2005).

4.2. Economic importance of mangrove-associated fisheries

Fisheries production constitutes the major value of marketed natural resources from mangrove ecosystems. In terms of habitat use, the mangrove support to commercial, recreational and subsistence fisheries is well documented (see review in Rönnbäck, 1999). For instance, 80% of all marine species of commercial or recreational value in Florida, USA, have been estimated to depend upon mangrove estuarine areas for at least some stage in their life cycles (Hamilton and Snedaker, 1984). The relative contribution of mangrove-related species to total fisheries catch can also be significant, constituting 67% of the entire commercial catch in eastern Australia (Hamilton and Snedaker, 1984), 49% of the demersal fish resources in the southern Malacca Strait (Macintosh, 1982), 30% of the fish catch and almost 100% of shrimp catch in ASEAN countries (Singh et al., 1994).

Non-marketed catch is never included in fishery statistics, although coastal subsistence economies in many developing countries harvest substantial amounts of fish and shellfish from mangroves (Fig. 1F). The contribution of subsistence fisheries to total catch supported by mangroves was estimated at 10–20% in Sarawak (Bennett and Reynolds, 1993), 56% in Fiji (Lal, 1990), and 90% in Kosrae (Naylor and Drew, 1998). The annual subsistence harvest per household has been valued at US$610 in Fiji (Lal, 1990) and $900 in Irian Jaya, Indonesia (Ruitenbeek, 1994). For the poorest coastal families, mangrove fisheries clearly have an emergency food provision function and constitute the main source of protein in their diet (Magalhaes et al., 2007).

The most frequently used method to assess the mangrove support to commercial fisheries is the production function approach, where mangroves are put in as a determinant for fisheries catch (Barbier, 1994, 2003). Positive correlations between offshore yield of penaeid shrimps and amount of mangrove forest in the nursery area have been demonstrated throughout the tropics (e.g., Turner, 1977; Pauly and Ingles, 1986; Baran and Hambrey, 1998; Lee, 2004), whereas studies on other crustaceans, fish and molluscs are scarce (Rönnbäck, 1999). Correlations have been found between penaeid catches and latitude (inversely proportional) by Turner (1977) and Pauly and Ingles (1986), and with extent of intertidal areas and tidal amplitude (Lee, 2004). Furthermore, Pauly and Ingles (1986) found a non-linear logarithmic relationship between mangrove area and penaeid shrimp production, implying that the shrimp fisheries impact of reducing mangrove area becomes greater as the remaining area is reduced. Similarly, the length of mangrove-lined estuary or habitat edge where juvenile prawns have access to the mangrove is a more important indicator of shrimp densities than total area per se (Staples et al., 1985; Chong, 2007).

Quantitative estimates of fisheries production supported by mangroves have mainly focused on penaeid shrimps (e.g., Christensen, 1982; Lal, 1990; Ruitenbeek, 1994; Barbier and Strand, 1998), and there is a severe lack of productivity and monetary estimates for other fisheries (Nickerson, 1999; Rönnbäck, 1999). This may be related to the varying degree of mangrove importance as nurseries for fish, especially in the presence of alternative habitats like seagrass beds (Robertson and Duke, 1990a; Nagelkerken et al., 2000, 2002; Nagelkerken and van der Velde, 2004). To identify and value total commercial and subsistence fisheries catch supported by mangroves, economic analyses must take into account: (1) the large number of resident and transient species that utilize mangroves as habitat; (2) the biophysical interactions in the coastal seascape biome; (3) the direct and indirect subsidies of shrimp trawlers and mangroves, respectively, to total fisheries catch; and (4) the aquaculture industry's dependence on inputs like seed, broodstock and feed (Rönnbäck, 1999). By acknowledging these support functions, the potential life-support value of mangroves to fisheries is in the order of 1–10 tons of fish and shellfish per ha and year (first sale value ≈ 1000–10,000 US$ in developing countries) (Rönnbäck, 1999).

5. Mangrove ecosystem services

Mangroves support a wide variety of ecosystem services (e.g., Saenger et al., 1983; Ewel et al., 1998a; Moberg and Rönnbäck, 2003; Barbier, 2007; Rönnbäck et al., 2007a), which can be classified into supporting, provisioning, regulating and cultural services (Millennium Ecosystem Assessment, 2005). Supporting services are those that are necessary for all other ecosystem services, and include soil formation, photosynthesis, primary production, nutrient cycling and water cycling. Provisioning services are the natural products generated by mangroves (see previous sections).

Regulating ecosystem services are the benefits obtained from the regulation of ecosystem processes such as resilience, pollination, biological control, nutrient cycling, air quality regulation, and maintenance of biodiversity for ecosystem function and resilience, etc. (Millennium Ecosystem Assessment, 2005; Rönnbäck et al., 2007b; Bosire et al., 2008; Cannicci et al., 2008; Gilman et al., 2008; Kristensen et al., 2008; Nagelkerken et al., 2008). Regulating services analyzed in detail below include water quality maintenance, environmental disturbance prevention (storm, flood and erosion control) and climate regulation. One critical function supporting all these services is that mangroves effectively retard water flow, mainly as a function of the trees' three-dimensional structural complexity and the complex topographical features of channels, creeks, etc. This enables efficient trapping of suspended and particulate matter, which can lead to land accretion buffering against potential sea level rise in the future.

Favorable sediment characteristics and high photosynthetic rates of many mangrove systems provide the basis for the biofilter function with high nutrient uptake levels (Rivera-Monroy et al., 1995; Robertson and Phillips, 1995; Alongi et al., 2000). Peri-urban coastal areas of the developing world receive extensive amounts of untreated sewage, and mangroves certainly filter this discharged wastewater, thereby limiting coastal sewage pollution. Based on the cost of constructing a sewage treatment plant, the value of biofilter functions of mangroves has been estimated at US$ 1193 ha^{-1} $year^{-1}$ to US$ 5820 ha^{-1} $year^{-1}$ depending on types and extent of mangroves (Table 2). The wide-scale conversion of mangroves to accommodate shrimp farms removes the natural biofilter function of surrounding mangroves. Consequently, waste laden pond effluent water is reused causing self-pollution (Rönnbäck, 1999; Kautsky et al., 2000) in the farm system itself, but also affecting remaining mangroves and littoral habitats, often of primary importance for collection of marine products by local communities. Robertson and Phillips (1995) estimated that up to 22 ha of mangrove forest would be required to filter the nutrient load per hectare of intensive shrimp pond. More recently, Primavera et al. (2007) showed that 1.8–5.4 ha of mangroves are required to remove nitrates in effluents from 1 ha of shrimp pond.

Mangroves are considered as a natural barrier protecting the lives and property of coastal communities from storms and cyclones, flooding, and coastal soil erosion (Farber, 1987; Othman, 1994; Sathirathai and Barbier, 2001; Lal, 2002; Walters, 2003, 2004; Badola and Hussain, 2005; Hong, 2006; Barbier, 2007). Values ascribed to this service include, for example, US$ 120 per household (Badola and Hussain, 2005), and US$ 3700 ha^{-1} (Sathirathai and Barbier, 2001) and US$ 4700 ha^{-1} (Costanza et al., 1989) of mangrove (Table 2). These are major indirect benefits and a principal reason for planting mangroves along many low-lying coasts. Artificial structures to replace the coastal protection services provided by mangroves can be expensive (Moberg and Rönnbäck, 2003; Walters, 2003) and may not be as effective (Badola and Hussain, 2005; Barbier, 2006).

In particular, the Indian Ocean Tsunami disaster of December 26, 2004, which killed over 200,000 people and damaged livelihoods and coastal resources in 14 Asian and African countries, highlighted the role of protection and sound management of the coastal environment and provided a stark reminder that environmental sustainability and human security are inseparable (Walters, 2006).

The tsunami disaster has received scientific and media attention worldwide, and the protective function of mangroves for landward human settlements has been often highlighted. Yet, most reports with respect to protection by mangrove forests were either very localized and/or anecdotal in nature (Danielsen et al., 2005; Harakunarak and Aksornkoae, 2005; IUCN, 2005; Liu et al., 2005; Roy and Krishnan, 2005; Williams, 2005; Dahdouh-Guebas, 2006; Stone, 2006; Wells and Kapos, 2006). This has prompted two, contradicting 'narratives' among authors and policy-makers regarding the protective role of mangroves. On one hand, some have generalised the protective function of mangroves as documented from some areas to entire coastlines and countries and therefore over-interpreted the role of mangroves. On the other hand, others have generalised the apocalyptical nature of a tsunami based on the Banda Aceh experience and minimalised the role of mangroves to the extent of suggesting that they are ineffective and that more effort should be focused on tsunami alert systems (Overdorf and Unmacht, 2005; Baird, 2006). Both views have been criticized because of insufficient examination of results or assumptions supporting this function (Dahdouh-Guebas et al., 2005c; Kathiresan and Rajendran, 2005; Dahdouh-Guebas and Koedam, 2006).

The role of mangroves in wave attenuation has long been scientifically proven (Furukawa et al., 1997; Wolanski, 1995; Mazda et al., 1997; Massel et al., 1999). Reduction of waves depends on water depth, wave period and height, quality of the mangrove forest, and type of aerial root systems (Mazda et al., 1997; Kathiresan, 2003; Dahdouh-Guebas et al., 2005c). The post tsunami studies have found that human deaths and loss of property was a function of type and area of the coastal vegetation shielding the villages (Dahdouh-Guebas et al., 2005c; Kathiresan and Rajendran, 2005; but see Kerr and Baird, 2007). Further evidence of the storm protective value of mangroves can be found in studies of local peoples' knowledge and practices. Among some coastal communities in the Philippines and India there is a widely-held appreciation for the storm protective function of mangroves, and many people plant and protect mangrove trees explicitly for this purpose (Fig. 1A; Walters, 2003, 2004; Badola and Hussain, 2005; Walton et al., 2006b). It is common practice for small-boat fishers in these countries to seek the shelter of mangroves during storms, but sheltering in deep mangrove creeks also provided protection to commercial, recreational and naval vessels in the port of Cairns, Australia when tropical cyclone Larry crossed the Queensland coast on 20 March 2006 (Williams et al., 2007). Some earlier studies have also suggested that the loss of lives due to hurricanes, tidal waves, typhoons, etc. could have been reduced by the presence of a mangrove protective belt (Fosberg, 1971; Primavera, 1995; Mazda et al., 1997; Massel et al., 1999).

Mangrove ecosystems are among the most productive and biogeochemically active ecosystems and represent potentially important sinks of carbon in the biosphere (Twilley et al., 1992; Ong, 1993; Gattuso et al., 1998). Clough et al. (1997) calculated net photosynthetic rates of 155 kg C ha^{-1} per day in a 22-year old *Rhizophora apiculata* Bl. forest in Malaysia (Table 2). The carbon stock per unit area can also be enormous as the top layers of mangrove sediments store large amounts of organic carbon, typically an order of magnitude higher than those of other tropical forests. Successful management of mangrove ecosystems thus has the potential to produce a 'measurable' gain in CO_2 sequestration (Ayukai, 1998), a characteristic likely to acquire greater attention with the forecasted global warming this century.

Cultural services stem from dynamic and complex social attributes. The variety within coastal ecosystems provides humans with almost unlimited opportunities for aesthetic and recreational experiences, cultural and artistic inspiration, as well as spiritual and religious enrichment (Fig. 1B; Mastaller, 1997; Kaplowitz, 2001; Rist and Dahdouh-Guebas, 2006; Rönnbäck et al., 2007b). An intriguing illustration comes from the *Asmat* from Irian Jaya, Indonesia, who have largely preserved their traditions and beliefs (Mastaller, 1997). According to their legends, their creator carved human-like figurines out of a mangrove root which came to life when he played a self-made drum out of a mangrove tree (loc. cit.). Today, *Rhizophora* roots are still used to carve mystic totem poles (loc. cit.).

The location of mangroves along the coastline, often proximate to populated areas, combined with their unique ecological and aesthetic character, affords opportunities for development of eco-tourism and environmental education. Many coastal communities have co-evolved with their local mangrove ecosystems. Their traditional use of mangrove resources is often intimately connected with the health and functioning of the system. These uses are often governed by customary rights, traditions and heritage, and they are often closely tied to the culture of the local communities. The failure to recognize these customary use rights has often resulted in the alienation of local communities in managing local mangrove ecosystems, and in participating in the replanting and rehabilitation of mangroves (Walters, 2004; Barbier, 2006), subsequently undermining incentives for, and use of, LEK which could be valuable for management purposes.

6. Mangrove management, planning and policy

6.1. Property rights, resource access and conflict

Mangroves are unusual environments in that they are located between dry land and shallow marine and brackish water. This characteristic introduces complexities to planning and management because of competing and overlapping interests in mangrove lands and their resources. In short, mangroves are valuable coastal lands to various forest users and land developers, each one having incentive to claim and control access through degrees of privatization. But this tenure dynamic changes because marine and estuarine waters in mangroves as elsewhere are typically viewed as open access transportation corridors for fishing boats, and the diverse fish and crustaceans within these waters are usually treated as a common property resource available for harvest by local fishermen.

These complexities are often mirrored in government policy. Until recently, most governments considered mangroves to be relatively worthless swamplands, so rational policy guiding their management has in most cases been late in coming. Being part land and part sea, jurisdictional ambiguities are often present. For example, regulation of mangrove forest lands in the Philippines has historically fallen under the legal jurisdiction of both the Department of Environment and Natural Resources (formerly the Ministry of Forests), whose mandate was to protect and sustainably manage these as forests, and the Department of Agriculture, whose mandate was to promote brackish water aquaculture development in these same areas (Primavera, 2000a, 2005; Walters, 2003). Thus, government decisions concerning mangroves were often made with "...the right hand not knowing what the left hand was doing" (Primavera, 1993, p. 168). Similar problems of jurisdictional ambiguity over mangroves have been documented in Ecuador (Meltzoff and LiPuma, 1986), India (Bhatta and Bhat, 1998; Dahdouh-Guebas et al., 2006a), Thailand (Vandergeest et al., 1999), Sri Lanka (Dahdouh-Guebas et al., 2000a, b), Indonesia (Armitage, 2002) and Brazil (Glaser and Oliveira, 2004).

But such ambiguities go beyond government policy and affect informal understandings and customary rules concerning access and use of mangroves by different users. Customary use of mangroves is typically characterized by common access rights, with different uses overlapping but to a large degree accommodating one another (Fig. 1E; Bhatta and Bhat, 1998; Walters, 2004). Conflict in such situations can arise, for example, where customary boat access or seine fishing rights become impaired by the construction of a dyke or the planting of mangrove trees (Walters, 2004), or where resident mangrove fishers and wood users are forced to compete with outsiders for the same resources (Glaser and Oliveira, 2004). The potential for such conflict is exacerbated where large tracts of mangrove are leased to private interests who displace common access users (Bailey, 1988; Dewalt et al., 1996; Stonich and Bailey, 2000; Walters, 2003, 2004; Hoq, 2007). The issue of shrimp farming is particularly problematic because the large profit potential of these operations creates incentive for corruption of legal mechanisms that might otherwise protect the forests and/or interests of local users (Meltzoff and LiPuma, 1986; Bhatta and Bhat, 1998; Stonich and Vandergeest, 2001; Armitage, 2002; Dahdouh-Guebas et al., 2002). In short, conflict is more likely to emerge in the absence of shared understandings about rules of access, clear government regulations, and effective means of enforcement and dispute resolution.

6.2. Deforestation and competing land uses

Mangrove forests are among the most threatened global ecosystems, especially in Asia, and current mangrove area has fallen below 15 million hectares, down from 19.8 million ha in 1980 (Wilkie and Fortuna, 2003). Global rates of loss in the past two decades vary from 20% (Wilkie and Fortuna, 2003) to 35% (Valiela et al., 2001). The average rate of 1.52% mangroves lost per year (Valiela et al., 2001; Alongi, 2002) shows an improvement from 1.9% in the 1980s to 1.1% in the 1990s (Wilkie and Fortuna,

Table 2
Examples of economic assessments of some regulating ecosystem services supported by mangroves

Regulating service	Values and benefits	Reference
Water quality maintenance (biofilter function)	US$ 5820 ha^{-1} year^{-1}	Lal, 1990
	US$ 1193 ha^{-1} year^{-1}	Cabrera et al., 1998
	7.4 and 21.6 ha of mangroves needed to remove nitrate and phosphorous, respectively, in effluents per ha of intensive shrimp pond	Robertson and Phillips, 1995
	1.8–5.4 ha of mangroves needed to remove nitrate in effluents per ha of shrimp pond	Primavera et al., 2007
Environmental disturbance prevention (storm, flood and erosion control)	US$ 4700 ha^{-1}	Costanza et al., 1989
	US$ 3679 ha^{-1}	Sathirathai and Barbier, 2001
	US$ 120 per household	Badola and Hussain, 2005
Carbon sink	155 kg C ha^{-1} day $^{-1}$	Clough et al., 1997
	1500 kg C ha^{-1}	Ong, 1993

2003). Nevertheless, the prospect of a world without mangroves appears to be real (Duke et al., 2007). Although many factors are behind global mangrove deforestation, a major cause is aquaculture expansion in coastal areas, especially the establishment of brackish water fish and shrimp farms (Primavera, 1995; Barbier and Cox, 2003). Aquaculture accounts for 52% of mangrove loss globally, with shrimp farming alone accounting for 38% of mangrove deforestation; in Asia, aquaculture contributes 58% to mangrove loss with shrimp farming accounting for 41% of total deforestation (see Table 3 in Valiela et al., 2001). Other factors in mangrove decline are forest use, mainly for industrial lumber and woodchip operations (26%), freshwater diversion (11%), and reclamation of land for other uses (5%). The remaining causes of mangrove deforestation are herbicide impacts, agriculture, salt ponds and other coastal developments. A global survey of 38 coastal, island and estuarine mangrove stands confirmed that clear cutting and reclamation for agriculture and aquaculture, urban expansion and resort development threatened the majority (55%) of all sites visited (Farnsworth and Ellison, 1997).

The conversion of mangroves to aquaculture ponds has been fuelled by governmental support, private sector investment and external assistance from multilateral development agencies such as the World Bank and Asian Development Bank (Siddall et al., 1985; Verheugt et al., 1991). To quote a report of the 1978 Aquaculture Project in Thailand “The subproject will involve the large-scale development of mangrove swamps into small shrimp/fish pond holdings . . .” (ADB, 1978 in Primavera, 1998a). From US $368 million (representing only 14.1% of total fisheries assistance) in 1978–1984, international aid to aquaculture increased to $910 million (33.7% of total fisheries assistance) in 1988–1993 (Primavera, 1998a). The Asian Development Bank alone provided total aid to fisheries and aquaculture of $1085 million in the 1969–1996 period, including US $21.8 million in aquaculture loans for shrimp and milkfish ponds and hatcheries in the Philippines (Primavera, 1998a, 2000b). But the much earlier fishpond boom of the 1950s was fuelled by a loan of US$ 23.6 million for fishpond construction and operations from the International Bank for Reconstruction and Development intended “to accelerate . . . the conversion of vast areas of marshy lands [mangroves] . . . into productive fishponds” (Villaluz, 1953, in Primavera, 2000a).

The effects of this decline in mangrove area are exacerbated by the widespread degradation of remaining forests, the result of over-cutting of wood and over-harvesting of mangrove aquatic resources. The extent of such degradation is not well documented, but case studies reveal dramatic changes to the structure and composition of harvested forests and associated declines in resource availability to local communities (Kairo et al., 2002; Walters, 2005b). Infrastructure developments and upland land use can cause sedimentation and changes to hydrology that impact mangroves at some distance, causing the gradual die-back of particular species or entire stands (Dahdouh-Guebas et al., 2005b). Ironically, such ecological degradation can be masked by the expansion of less typical, less functional and less vulnerable species and thus take the form of ‘cryptic ecological degradation’ (sensu Dahdouh-Guebas et al., 2005b).

Problems of deforestation and degradation are compounded by growing human populations in many coastal areas (Primavera, 2000a). The Philippines offers a case in point: mangroves once abundant around Manila Bay at the turn of the last century have since been entirely cleared, the combined result of fish pond development, urban infrastructure expansion and residential spread (Brown and Fischer, 1918; Cabahug et al., 1986). Similarly, in a more rural region of the country, Bais Bay, mangroves have declined in area over the past 50 years by 75% at the same time that coastal populations have increased 10-fold (Walters, 2003). Population growth coinciding with declining mangrove area has likewise been documented along the coastlines of Honduras (Dewalt et al., 1996), Vietnam (de Graaf and Xuan, 1998) and Bangladesh (Bashirullah et al., 1989).

6.3. *Mangrove silviculture*

Mangrove silviculture has been practiced in some Asian countries since the 19th century (Brown and Fischer, 1918; Watson, 1928; Curtis, 1933; Hussain and Ahmed, 1994; Kaly and Jones, 1998; Vannucci, 2002). Mangroves are planted for various purposes, including (i) wood production to support commercial or small-scale forestry; (ii) shoreline protection, channel stabilization and storm protection for coastal human settlements from cyclones and other extreme natural events, and for protection against seawater intrusion; (iii) fisheries, aquaculture and wildlife enhancement; (iv) legislative compliance with protective measures and compensatory requirements; (v) social enrichment (e.g., aesthetics, income generation through eco-tourism); and (vi) ecological restoration (Field, 1996; Bhatta and Bhat, 1998; Kairo et al., 2001; Walters, 2004; Walters et al., 2005). Nursery and planting techniques vary considerably among mangrove species, and the silvicultural methods chosen will depend on which of the above objectives are desired (Field, 1998; Saenger, 2002).

Traditionally, both clear-felling and selection systems have been used, and in some areas a mixed system has been employed (FAO, 1994). Clear-felling systems applied to mangrove forests are the most cost-effective, although erosion and site deterioration risks as well as the loss of ecosystem services are higher. Clear-felling has been found suitable for some economically valuable species, such as *Rhizophora apiculata*, *R. mucronata* Lamk. and

R. stylosa Griff., which are strong and light-demanding and so can withstand competition in open areas. In selection systems, the stands are uneven-aged and the forest cover is never completely removed. They are more environment-friendly since marketable trees are harvested periodically and over all parts of the forests, providing better soil protection and biodiversity, reducing risks of insect damage and invasions, and offering improved wind buffering. However, selection systems are less cost-effective due to their complexity and greater labor requirements.

Mangrove silvicultural practices have produced mixed results depending on the practices. For example, the success of mangrove management since the beginning of the 20th century in Matang, Malaysia is mainly due to intensive reforestation efforts (Ong, 1995; Chan, 1996), although decline in yields has been reported since the late 1960s (Gong et al., 1980; Gong and Ong, 1995). Likewise, multi-use managed forests in the Sunderbans have maintained long-term productivity through the application of scientific silvicultural practices with traditional knowledge (Vannucci, 2002). In Venezuela, however, the Guarapiche Forest Reserve, San Juan River is yet to recover fully despite well-planned silvicultural practices (Lacerda et al., 2002). Although restored mangrove forests may resemble forest plantations rather than natural forests, such plantations can be a first step toward mangrove rehabilitation (Ellison, 2000; Bosire et al., 2003; Bosire et al., 2008; but see Walters, 2000). To improve the success in rehabilitation, other silvicultural methods have been employed including natural regeneration, assisted regeneration and macro-propagation.

Reforestation of mangrove forests through natural regeneration is relatively inexpensive and maintenance is less labor-intensive. Natural regeneration leads to better early root development and causes less soil disturbance. However, the success of natural regeneration will depend on the state of degradation of the original mangrove. Although assisted regeneration is more expensive, its costs will vary depending on labor costs, site characteristics, proximity to propagule sources, and whether propagules, seedlings or transplants are used (Saenger, 1996). Assisted regeneration may be required at sites with insufficient natural regeneration. Approaches for macro-propagation of mangroves include direct planting of propagules collected from the wild, out-planting of up to 1-year-old nursery-raised propagules, direct transplanting of seedlings and shrubs, out-planting after nursery-raising small seedlings collected from the wild, raising of air-layered material, and use of stem cuttings (Carlton and Moffler, 1978; Hamilton and Snedaker, 1984; Field, 1996).

6.4. Ecological restoration

Ecosystem restoration to the original pristine state, or rehabilitation to recover some ecosystem functions, may be appropriate when a mangrove ecosystem has been altered so that normal processes of secondary succession or natural recovery from damage are inhibited in some way. Mangrove restoration is increasingly practiced in many parts of the world (Ellison, 2000; Kairo et al., 2001; Vannucci, 2002). Mangrove forests have been rehabilitated to achieve a variety of goals, e.g., for commercial purposes (Watson, 1928), restoring fisheries and wildlife habitat (Lewis, 1992; Stevenson et al., 1999), multiple community use purposes, or shoreline protection purposes (Thorhaug, 1990; Saenger and Siddiqi, 1993; Bhatta and Bhat, 1998; Field, 1998; Walters, 2004; Barbier, 2006; Walton et al., 2006b).

There is already a great deal of knowledge and experience in rehabilitating mangroves by artificial means around the world (Field, 1996, 1998). However, many of these efforts are carried out without considering the experience and lessons learned from similar projects, resulting in duplication of efforts and waste of resources (Elster, 2000; Kairo et al., 2001). Recently, interest has focused on indigenous or folk technologies for mangrove restoration. For example, local fisherfolk have been planting mangroves in some areas of Southeast Asia for decades, well before governments and non-government organizations began to promote the activity as a conservation tool (Fig. 1E; Fong, 1992; Weinstock, 1994; Walters, 2000, 2004). These local management systems are relatively small-scale and utilize simple technologies, but they can be rich in knowledge and practical experience that is usually overlooked by ‘‘experts’’ who promote mangrove reforestation (Vayda et al., 2004; Walters, 1997; Walters et al., 2005).

Failure to better understand the local environmental and socio-economic contexts of mangrove restoration dooms many such efforts. Mangrove restoration projects often have moved immediately into planting of mangroves without determining the cause of previous degradation or why natural recovery has failed (Lewis, 2000, 2005). Even where environmental conditions permit natural or assisted restoration of a site, ongoing or future disturbance of the area by local people may prevent it (Walters, 1997). Ideally, mangrove restoration success should be measured as the degree to which the functional replacement of natural ecosystem has been achieved. However, long-term success in mangrove replanting will be determined by the level of support and involvement of local communities and local governments (Primavera and Agbayani, 1997; Walters, 1997, 2004; Lewis, 2000; Barbier, 2006). Mangrove rehabilitation programs that only utilize coastal communities as sources of replanting labor and do not involve them in the long-run management of the various uses of the restored ecosystem are less likely to be successful (Rönnbäck et al., 2007a).

A review of mangrove (re)planting in the Philippines over the past century shows a change from community-led efforts to projects externally driven by international development grants and loans. This change in drivers is paralleled by an increase in planting costs from <\$100 ha^{-1} to over \$500 ha^{-1}, yet long-term survival rates generally remain low. Poor survival can be traced to inappropriate species (*Rhizophora* is favored over the natural colonizers *Avicennia* and *Sonneratia* because it is easier to plant), and unsuitable sites in open access but suboptimal lower intertidal to subtidal zones, rather than the ideal but contentious middle to upper intertidal areas which have long been converted to aquaculture ponds. For mangrove rehabilitation efforts to succeed, funding appears to be of secondary importance relative to suitable sites and species, community involvement and commitment, and grant of tenure.

6.5. Geo-spatial monitoring and analysis

In order to develop and implement effective policy regarding the socio-economic use of mangrove forests, it is essential that stakeholders have access to accurate and cost-effective techniques for mapping and monitoring these coastal wetlands. Given that many of these forests are quite large, are located in remote areas and have been experiencing rapid changes, it is not surprising that various remote sensing techniques have been employed to determine their spatial distribution and health. Traditional aerial photography is still being employed (e.g., Krause et al., 2004; Dahdouh-Guebas et al., 2006b) to map these forests, but given their repetitive coverage with constant image quality and immediate ease of operation, the use of satellite imagery, both optical and radar, now govern this endeavor. Satellite imagery enables resource managers to quickly map and continuously monitor their mangroves without the constant need for exhaustive field surveys. Using very high resolution imagery, the development of single species or even trees can be monitored, which may be necessary in light of selective cutting and ecological degradation (Dahdouh-Guebas et al., 2005a). Moreover, these digital data are easily transferable into Geographic Information Systems for spatial analyses studies at a broader coastal management level.

There are two types of space-borne data available for mangrove forest mapping, optical and radar. Optical sensors rely on reflected sunlight, primarily in the visible and infra-red regions of the electromagnetic spectrum. With regards to mangroves, the signals received can provide information regarding the photosynthetic activity of the trees which can then be used to distinguish them from other non-mangrove land covers or even between mangrove species or mangrove conditions (e.g., unhealthy stands). Conversely, Synthetic Aperture Radar (SAR) satellites actively emit microwave energy to their targets. The returning radar signals from the surface (i.e. backscatter) are very sensitive to dielectric and geometric properties of mangrove canopies and can thus also be used as an alternative or supplement to optical mapping procedures.

To date the vast majority of investigations using space-borne platforms to map and monitor mangroves have focused on optical sensors, primarily from the traditional/conventional SPOT and Landsat satellite series. These satellites have been used to map mangroves in a myriad of countries including, for example, Australia (Long and Skewes, 1996), Brazil (Brondizio et al., 1996), New Zealand (Gao, 1998), Thailand (Webb et al., 2000), the Turks and Caicos Islands (Green et al., 1998), the United Arab Emirates (Saito et al., 2003) and Vietnam (Tong et al., 2004). In comparison to the recent launch of very high resolution optical satellites (e.g., IKONOS in 1999), these traditional sensors are limited in spatial resolution (e.g., ~1 m versus ~25 m pixel size). However, these satellite data are cheaper, provide a larger coverage per acquisition, are easier to process and have extensive records (e.g., Landsat data extending back to 1972).

Consequently, they continue to play a very crucial role in assessing historical changes in mangrove forests. For example, multi-temporal SPOT and multi-temporal Landsat images have been used to determine the rates of mangrove forest degradation occurring in Madagascar (Rasolofoharinoro et al., 1998) and Mexico (Kovacs et al., 2001a), respectively, both resulting from hydrologic modification incurred from channel projects. Rates of mangrove gradation and degradation resulting from natural cycles of coastal accretion and erosion have also been determined for the coast of French Guiana using multi-date SPOT satellite data (Fromard et al., 2004) and for the Para coastline (North Brazil) using multi-date Landsat data (Cohen and Lara, 2003). Multi-temporal satellite data have even been used to quantify the success of mangrove forest recovery resulting from the implementation government regulations on mangrove protection in Thailand (Muttitanon and Tripathi, 2005) and from very recent mangrove reforestation projects initiated by the Red Cross in Vietnam (Beland et al., 2006).

One major limitation to the use of the conventional sensors has been the inability to distinguish mangroves at the species level. In the aforementioned studies, mangroves are either simply separated from non-mangrove land cover/land use areas or they are further subdivided into 2–7 broad qualitative mangrove classes such as dense/tall or short/sparse mangroves. In a few circumstances, tall dense Rhizophora species have been mapped using Landsat data. Such mapping scales may suffice for many mangrove policy and management programs, especially in countries where only one species exists (e.g. New Zealand), but they could seriously hinder efforts where socio-economic policies on mangroves are based at the species level. Fortunately, studies in Panama (Wang et al., 2004a, b), Mexico (Kovacs et al., 2005) and Sri Lanka (Dahdouh-Guebas et al., 2005a) have shown that with the very high resolution optical satellites (IKONOS and Quickbird) mangroves can be accurately mapped at the species level from space.

Whilst the number of studies is extremely limited, researchers have shown that space-borne SAR can be used in conjunction with optical data or as an alternative in the mapping of mangroves (Aschbacher et al., 1995; Dwivedi et al., 1999; Kushwaha et al., 2000; Simard et al., 2002). The main advantages of SAR are that it is not limited to daylight and, most importantly, it can penetrate cloud cover. Consequently, in cloud persistent areas of the tropics, it may be the only viable method for mangrove monitoring. Moreover, depending on the polarization, incidence angle and wavelength, SAR can penetrate forest canopies providing additional information that is not possible from optical sensors. The studies of space-borne SAR have, to date, been limited to older SAR satellites which are limited not only in spatial resolution but in flexibility of incidence angle and polarization mode acquisition options. With the recent launch of a new generation of SAR satellites (e.g., C-band Radarsat-2, L-band ALOS Palsar), it is anticipated that, with their technological advancements (e.g., fully polarimetric capabilities), SAR mangrove mapping accuracies will dramatically improve.

Thus far, all of the studies cited have indicated that mangrove aerial extent can be mapped accurately from space and that these sensors can provide an effective method for long-term mangrove monitoring. However, in some circumstances, resource managers and policy-makers may require quantitative data (i.e., biophysical parameters) of their mangrove forests including measures of tree height, basal area, stem density and even biomass indicators such as Leaf Area Index (LAI) and allometric equations (cf. Komiyama et al., 2008). For example, they may wish to model the ecological response of a mangrove forest to hurricanes (Kovacs et al., 2001b) or determine how the biophysical parameters of their mangrove are modified by local cuttings (Walters, 2005b). Quantitative studies using remote sensing techniques require, initially, a significant amount of field data collection and are thus labor-intensive and expensive to conduct and possibly why so few of these studies are available.

With regards to conventional optical satellite data, significant relationships have been found between SPOT vegetation indices and both mangrove percent canopy closure (Jensen et al., 1991) and mangrove LAI (Green et al., 1997). Using simulated data, results from one study (Ramsey and Jensen, 1996) have also indicated that vegetation indices derived from Landsat and AVHRR data can also be correlated with mangrove LAI. More recently, significant relationships between mangrove LAI and IKONOS data have also been established (Kovacs et al., 2004a, b). Consequently, this parameter can now be estimated from optical satellite data at even the species level (Kovacs et al., 2005). As previously indicated, SAR can not only provide information on the geometry and water content of forest canopies but, in some circumstances, even collect data from below the canopy layer. For example, although using airborne and not space-borne SAR, researchers (Mougin et al., 1999) in French Guiana have found not only significant relationships with radar backscatter and both mangrove height and biomass but also with mangrove stem density and basal area. With regards to space-borne SAR platforms, significant relationships have also been found between radar backscatter and mangrove LAI using both Radarsat-1 (Kovacs et al., 2006) and ENVISAT ASAR (Kovacs et al., 2008) satellite data. It is again anticipated that with the new generation of SAR satellites other mangrove forest biophysical parameter data could be extracted using radar backscatter signals.

Given the aforementioned advances in Earth observational imaging, it is no surprise that the availability of these data have significantly improved the ability of policy-makers and resource managers to monitor socio-economic impacts on their mangrove forests. Moreover, and possibly just as important, is the availability of these data to the general public. Specifically, satellite imagery, although in a limited format (e.g., limited spectral resolution), are now available on internet free access virtual globe programs such as Google Earth. In the hands of the public, these new tools could significantly alter the socio-economic dynamics associated with these forests at even the most local of scales.

7. Conclusions and future directions

Research on the human dimensions of mangrove forests remains a relatively new frontier. While not intended to provide a comprehensive list of possible research topics, these concluding comments suggest several key priorities.

There are a growing number of studies which examine local resource utilization and valuation of mangroves, yet coverage is patchy: limited to a relatively small number of sites, concentrated within a few biogeographic regions (esp. East Africa, Southeast Asia and the Indian subcontinent), and typically conducted over short time frames. Significant mangrove regions remain understudied (e.g., West Africa, South America, Indonesia). Furthermore, most of these studies exist in relative isolation from one another, yet opportunities to extract regional and global patterns are now warranted. Research that incorporates multi-year time frames and historical perspectives are particularly relevant given the rapid socio-economic and environmental changes unfolding along most tropical coastlines today. Likewise, there is need for economic valuation studies that explicitly focus on mangrove resources that are not marketed, but rather harvested and consumed directly by coastal households.

Studies that pay careful attention to the actual *ecology* of resource use are especially critical in light of the widespread influence of people on mangrove ecosystems (Walters, 2005b). Understanding how and why people actually harvest forest and aquatic resources in space and over time within a mangrove, and how these patterns of use impact the condition of the forest, is also vital for effective management, yet such information is almost always absent in planning and policy discussions. Standardised collection of this type of information from the local inhabitants is a first step in assuring that policy and law are anchored in local environmental and socio-economic reality (e.g., Kaplowitz, 2001; Omodei-Zorini et al., 2004; Walters, 2004; Dahdouh-Guebas et al., 2006a; Rist and Dahdouh-Guebas, 2006).

Location-specific studies should likewise be integrated with research that explicitly seeks to understand the range of human forces that impact mangroves less directly, but often more widely. Among these influences include (i) hydrological diversions caused by infrastructure developments along the coast or upstream of deltaic mangroves (e.g., dams); (ii) public policies with bearing on coastal natural resources, land use and development; (iii) markets for trade in mangrove products and products cultivated on former mangrove lands; and (iv) changes in sea level, rainfall and storm events associated with climate change.

The problems facing mangroves are dual: growing coastal populations put greater pressure on the ecosystem from the landward side, while global climate change, particularly sea-level rise, will increasingly put pressure on the mangrove from the seaward side. While the forest is squeezed as an ecosystem between these pressures, coastal subsistence users will be increasingly squeezed by economic pressures and public policies that respond to the same issues of overpopulation and global change. If resource management and land-use planning options to cope with these likely conditions are not effectively anticipated, both mangroves and the people who depend on them stand to lose.

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References

Adegbehin, J.O., 1993. Mangroves in Nigeria. In: Diop, E.S. (Ed.), Conservation and Sustainable Utilization of Mangrove Forests in Latin America and African Regions (Part 2: Africa). Mangrove Ecosystem Technical Reports 3, International Society for Mangrove Ecosystems and International Tropical Timber Organization, Tokyo, pp. 135–153.

Aksornkoae, S., Piebprom, S., Saraya, A., Kongsangchai, J., 1986. Mangrove resources and the socio-economics of dwellers in mangrove forests in Thailand. In: Kunstadter, P., Bird, E.C.F., Sabhasri, S. (Eds.), Man in the Mangroves. United Nations University, Tokyo, pp. 11–43.

Allen, J.A., Ewel, K.C., Keeland, B.D., Tara, T., Smith III, T.J., 2000. Downed wood in Micronesian mangrove forests. Wetlands 20, 169–176.

Allen, J.A., Ewel, K.C., Jack, J., 2001. Patterns of natural and anthropogenic disturbance of the mangroves on the Pacific island of Kosrae. Wetland Ecol. Manage. 9, 279–289.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Alongi, D.M., Tirendi, F., Trott, L.A., Xuan, T.T., 2000. Benthic decomposition rates and pathways in plantations of the mangrove *Rhizophora apiculata* in the Mekong delta, Vietnam. Mar. Ecol. Progr. Ser. 194, 87–101.

Alvarez-Leon, R., 1993. Mangrove ecosystems of Columbia. In: Lacerda, L.D. (Ed.), Conservation and Sustainable Utilization of Mangrove Forests in Latin America and African regions (Part 1: Latin America). Mangrove Ecosystem Technical Reports 2, International Society for Mangrove Ecosystems and International Tropical Timber Organization, Tokyo, pp. 75–114.

Armitage, D., 2002. Socio-institutional dynamics and the political ecology of mangrove forest conservation in Central Sulawesi, Indonesia. Global Environ. Change 12, 203–217.

Aschbacher, J., Ofren, R., Delsol, J.P., Suselo, T.B., Vibulsresth, S., Charrupat, T., 1995. An integrated comparative approach to mangrove vegetation mapping using advanced remote sensing and GIS technologies: preliminary results. Hydrobiologia 295, 285–294.

Ayukai, T., 1998. Introduction: carbon fixation and storage in mangroves and their relevance to the global climate change—a case study in Hinchinbrook Channel in northeastern Australia. Mangr. Salt Marsh. 2, 189–190.

Azariah, J., Selvam, V., Gunasekaran, S., 1992. Impact of past management practices on the present status of the Muthupet mangrove ecosystem. Hydrobiologia 247, 253–259.

Badola, R., Hussain, S.A., 2005. Valuing ecosystems functions: an empirical study on the storm protection function of Bhitarkanika mangrove ecosystem, India. Environ. Conserv. 32, 85–92.

Bagarinao, T.U., 1994. Systematics, genetics, distribution and life history of milkfish *Chanos chanos*. Environ. Biol. Fish. 39, 23–41.

Bagarinao, T.U., Primavera, J.H., 2005. Code of Practice for Sustainable Use of Mangrove Ecosystems for Aquaculture in Southeast Asia. SEAFDEC Aquaculture Department, Iloilo, Philippines, 47 pp.

Bailey, C., 1988. The social consequences of tropical shrimp mariculture development. Ocean Shore Manage. 11, 31–44.

Baird, A.H. 2006. Myth of green belts. Samudra Report 44, 14–19.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K., Turner, R.K., 2002. Economic reasons for conserving wild nature. Science 297, 950–953.

Bandaranayake, W.M., 1998. Traditional and medicinal uses of mangroves. Mangr. Salt Marsh. 2, 133–148.

Bandaranayake, W.M., 2002. Bioactivities, bioactive compounds and chemical constituents of mangrove plants. Wetland Ecol. Manage. 10, 421–452.

Baran, E., Hambrey, J., 1998. Mangrove conservation and coastal management in southeast Asia: what impact on fishery resources? Mar. Pollut. Bull. 37 (8–12), 431–440.

Barbier, E.B., 1994. Valuing environmental functions: tropical wetlands. Land Econ. 70, 155–173.

Barbier, E.B., 2003. Habitat-fishery linkages and mangrove loss in Thailand. Contemp. Econ. Policy 21, 59–77.

Barbier, E.B., 2006. Natural barriers to natural disasters: replanting mangroves after the tsunami. Front. Ecol. Environ. 4, 124–131.

Barbier, E.B., 2007. Valuing ecosystem services as productive inputs. Econ. Policy 22, 177–229.

Barbier, E.B., Strand, I., 1998. Valuing mangrove-fishery linkages: a case study of Campeche, Mexico. Environ. Res. Econ. 12, 151–166.

Barbier, E.B., Cox, M., 2003. Does economic development lead to mangrove loss? A cross-country analysis. Contemp. Econ. Policy 21, 418–432.

Barletta-Bergan, A., Barletta, M., Saint-Paul, U., 2002a. Community structure and temporal variability of ichthyoplankton in North Brazilian mangrove creeks. J. Fish Biol. 61, 33–51.

Barletta-Bergan, A., Barletta, M., Saint-Paul, U., 2002b. Structure and seasonal dynamics of larval fish in the Caeté River Estuary in North Brazil. Estuar. Coast. Shelf Sci. 54, 193–206.

Barnes, D.K.A., 2001. Hermit crabs, humans and Mozambique mangroves. Afr. J. Ecol. 39, 241–248.

Bart, D., 2006. Integrating local ecological knowledge and manipulative experiments to find the causes of environmental change. Front. Ecol. Environ. 4, 541–546.

Bashirullah, A.K.M., Mahmood, N., Matin, A.K.M.A., 1989. Aquaculture and coastal zone management in Bangladesh. Coast. Zone Manage. 17, 119–127.

Basit, M.A., 1995. Non-wood forest products from the mangrove forests of Bangladesh. In: Beyond timber: Social, economic and cultural dimensions of non wood forest products. Report 1995/13, Food and Agriculture Organization of the United Nations, Rome.

Beland, M., Goita, K., Bonn, F., Pham, T.T.H., 2006. Assessment of land-cover changes related to shrimp aquaculture using remote sensing data: a case study in the Giao Thuy District, Vietnam. Int. J. Remote Sens. 27, 1491–1510.

Bennett, E.L., Reynolds, C.J., 1993. The value of a mangrove area in Sarawak. Biodiv. Conserv. 2, 359–375.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Berkes, F., 1999. Sacred Ecology: Traditional Ecological Knowledge and Resource Management. Taylor & Francis, Philadelphia.

Berlin, B., 1973. Folk systematics in relation to biological classification and nomenclature. Ann. Rev. Ecol. Syst. 4, 259–271.

Bhatta, R., Bhat, M., 1998. Impacts of aquaculture on the management of estuaries in India. Environ. Conserv. 25, 109–121.

Bhattacharyya, J., 1990. Uses, values, and use values of the Sundarbans. Agric. Hum. Val. 7, 34–39.

Blanchard, J., Prado, G., 1995. Natural regeneration of *Rhizophora mangle* in strip clearcuts in Northwest Ecuador. Biotrop. 27, 160–167.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Koedam, N., 2003. Colonization of non-planted mangrove species into restored mangrove stands in Gazi Bay, Kenya. Aquat. Bot. 76, 267–279.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay. Biodiv. Conserv. 13 (6), 1059–1074.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Kazungu, J., Dehairs, F., Koedam, N., 2005a. Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya. Biol. Conserv. 126, 287–296.

Bosire, J.O., Kazungu, J., Koedam, N., Dahdouh-Guebas, F., 2005b. Predation on propagules regulates regeneration in a high-density reforested mangrove plantation. Mar. Ecol. Progr. Ser. 299, 149–155.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Wartel, S., Kazungu, J., Koedam, N., 2006. Success rates and recruited tree species and their contribution to the structural development of reforested mangrove stands. Mar. Ecol. Progr. Ser. 325, 85–91.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Brondizio, E., Moran, E., Mausel, P., Wu, Y., 1996. Land cover in the Amazon estuary: linking of the thematic mapper with botanical and historical data. Photogramm. Eng. Remote Sens. 62, 921–929.

Brown, W.H., Fischer, A.F., 1918. Philippine mangrove swamps. Bulletin No. 17, Bureau of Forestry, Department of Agriculture and Natural Resources, Manila.

Cabahug, Jr., D.M., Ambi, F.M., Nisperos, S.O., Truzan, Jr., N.C., 1986. Impact of community-based mangrove forestation to mangrove dependent families and to nearby coastal areas in Central Visayas: a case example. In: National Mangrove Committee (Ed.), Mangroves of Asia and the Pacific: Status and Management. Natural Resources Management Center, Ministry of Natural Resources, Quezon City, Philippines, pp. 441–466.

Cabrera, M.A., Seijo, J.C., Euan, J., Perez, E., 1998. Economic values of ecological services from a mangrove ecosystem. Intercoast Net. 32, 1–2.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Carlton, J.M., Moffler, M.D., 1978. Propagation on mangroves by air-layering. Environ. Conserv. 5, 147–150.

Chan, H.T., 1996. Mangrove reforestation in peninsular Malaysia: a case study of Matang. In: Field, C.D. (Ed.), Restoration of Mangrove Ecosystems. International Society for Mangrove Ecosystems, Okinawa, Japan.

Chang, L., Peng, L., 1987. Economic value of mangrove communities in China. In: Field, C.D., Dartnall, A.J. (Eds.), Mangrove Ecosystems of Asia and the Pacific: Status, Exploitation and Management. Australian Development Assistance Bureau and Australian Committee for Mangrove Research, Townsville, pp. 143–149.

Chapman, V.J., 1976. Mangrove Vegetation. Strauss & Cramer, Leutershausen, Germany.

Chong, V.C., 2007. Mangrove-fisheries linkages—the Malaysian perspective. Bull. Mar. Sci. 80, 755–772.

Chong, V.C., Sasekumar, A., Leh, M.U.C., D'Cruz, R., 1990. The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. Estuar. Coast. Shelf Sci. 31, 703–722.

Chong, V.C., Sasekumar, A., Wolanski, E., 1996. The role of mangroves in retaining penaeid prawn larvae in Klang Strait, Malaysia. Mang. Salt Marsh. 1, 11–22.

Christensen, B., 1982. Management and utilization of mangroves in Asia and the Pacific. FAO Environment Paper No. 3, Food and Agriculture Organization, Rome.

Christensen, B., 1983a. Report on Malaysia's mangrove management. Unasylva 35, 10–15.

Christensen, B., 1983b. Mangroves: what are they worth? Unasylva 35, 2–10.

Clough, B.F., Ong, J.E., Gong, W.K., 1997. Estimating leaf area index and photosynthetic production in canopies of the mangrove *Rhizophora apiculata*. Mar. Ecol. Progr. Ser. 159, 285–292.

Cohen, M.C.L., Lara, R.J., 2003. Temporal changes of mangroves vegetation boundaries in Amazonia: application of GIS and remote sensing techniques. Wetl. Ecol. Manage. 11, 223–231.

Cormier-Salem, M., 1999. The mangrove: an area to be cleared... for social scientists. Hydrobiologia 413, 135–142.

Costanza, R., Faber, C., Maxwell, J., 1989. The valuation and management of wetland ecosystems. Ecol. Econ. 1, 335–361.

Crona, B.I., 2006. Supporting and enhancing development of heterogeneous ecological knowledge among resource users in a Kenyan seascape. Ecol. Soc. 11 (1) art 32.

Crona, B.I., Rönnbäck, P., 2005. Use of replanted mangroves as nursery grounds by shrimp communities in Gazi Bay, Kenya. Estuar. Coast. Shelf Sci. 65, 535–544.

Crona, B.I., Rönnbäck, P., 2007. Community structure and temporal variability of juvenile fish assemblages in natural and replanted mangroves, *Sonneratia alba* Sm., of Gazi Bay, Kenya. Estuar. Coast. Shelf Sci. 74, 44–52.

Crona, B.I., Holmgren, S., Rönnbäck, P., 2006. Re-establishment of epi-biotic communities in reforested mangroves of Gazi Bay, Kenya. Wetland Ecol. Manage. 14, 527–538.

Curtis, S.J., 1933. Working Plans for the Forests of the Sundarbans Division for the Period From 1st April 1931 to 31st March 1951, vol. 1. Bengal Government Press, Calcutta, India.

Dahdouh-Guebas, F., 2006. Mangrove forests and tsunami protection. McGraw-Hill Yearbook of Science & Technology. McGraw-Hill Professional, New York, pp. 187–191.

Dahdouh-Guebas, F., Koedam, N., 2006. Coastal vegetation and the Asian tsunami. Science 311, 37–38.

Dahdouh-Guebas, F., Verheyden, A., De Genst, W., Hettiarachchi, S., Koedam, N., 2000a. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. Bull. Mar. Sci. 67, 741–759.

Dahdouh-Guebas, F., Mathenge, C., Kairo, J.G., Koedam, N., 2000b. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. Econ. Bot. 54, 513–527.

Dahdouh-Guebas, F., Zetterstrom, T., Rönnbäck, P., Troell, M., Wickramasinghe, A., Koedam, N., 2002. Recent changes in land use in the Pambala-Chilaw lagoon complex (Sri Lanka) investigated using remote sensing and GIS: conservation of mangroves vs. development of shrimp farming. Environ. Develop. Sustain. 4, 185–200.

Dahdouh-Guebas, F., Van Pottelbergh, I., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on retrospective remote sensing, social surveys, and distribution of trees. Mar. Ecol. Progr. Ser. 272, 77–92.

Dahdouh-Guebas, F., Van Hiel, E., Chan, J.C.-W., Jayatissa, L.P., Koedam, N., 2005a. Qualitative distinction of congeneric and introgressive mangrove species in mixed patchy forest assemblages using high spatial resolution remotely sensed imagery (IKONOS). Syst. Biodiv. 2, 113–119.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005b. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., Lo Seen, D., Koedam, N., 2005c. How effective were mangroves as a defense against the recent tsunami? Curr. Biol. 15, R443–R447.

Dahdouh-Guebas, F., Collin, S., Lo Seen, D., Rönnbäck, P., Depommier, D., Ravishankar, T., Koedam, N., 2006a. Analysing ethnobotanical and fishery-related importance of mangroves of East-Godavari Delta (Andhra Pradesh, India) for conservation and management purposes. J. Ethnobiol. Ethnomed. 2, art24.

Dahdouh-Guebas, F., Verheyden, A., Kairo, J.G., Jayatissa, L.P., Koedam, N., 2006b. Capacity building in tropical coastal resource monitoring in developing countries: a re-appreciation of the oldest remote sensing method. Int. J. Sustain. Develop. World Ecol. 13, 62–76.

Dall, W., Hill, B.J., Rothlisberg, P.C., Staples, D.J., 1990. The biology of the Penaeidae. Adv. Mar. Biol. 27, 1–489.

Danielsen, F., Sørensen, M.K., Olwig, M.F., Selvam, V., Parish, F., Burgess, N.D., Hiraishi, T., Karunagaran, V.M., Rasmussen, M.S., Hansen, L.B., Quarto, A., Suryadiputra, N., 2005. The asian tsunami: a protective role for coastal vegetation. Science 310, 643.

Davis, A., Wagner, J.R., 2003. Who knows? On the importance of identifying 'experts' when researching local ecological knowledge. Hum. Ecol. 31, 463–489.

de Graaf, G.J., Xuan, T.T., 1998. Extensive shrimp farming, mangrove clearance and marine fisheries in the southern provinces of Vietnam. Mangr. Salt. Marsh. 2, 159–166.

Dewalt, B.R., Vergne, P., Hardin, M., 1996. Shrimp aquaculture development and the environment: people, mangroves and fisheries on the Gulf of Fonseca, Honduras. World Develop. 24, 1193–1208.

Diop, E.S. (Ed.), 1993. Conservation and sustainable utilization of mangrove forests in Latin America and African regions (Part 2: Africa). Mangrove Ecosystem Technical Reports 3, International Society for Mangrove Ecosystems and International Tropical Timber Organization, Tokyo.

Duke, N.C., Meynecke, J.-O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Dwivedi, R.S., Rao, B.R.M., Bhattacharya, S., 1999. Mapping wetlands of the Sundarban Delta and it's environs using ERS-1 SAR data. Int. J. Remote Sens. 20, 2235–2247.

Ellison, A.M., 2000. Mangrove restoration: do we know enough. Restor. Ecol. 8, 219–229.

Ellison, A.M., Farnsworth, E.J., 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotrop. 28, 549–565.

Elster, C., 2000. Reasons for reforestation success and failure with three mangrove species in Columbia. For. Ecol. Manage. 131, 201–214.

Ewel, K.C., Twilley, R.R., Ong, J.E., 1998a. Different kinds of mangrove forests provide different goods and services. Global Ecol. Biogeogr. 7, 83–94.

Ewel, K.C., Zheng, S., Pinzon, Z., Bourgeois, J.A., 1998b. Environmental effects of canopy gap formation in high-rainfall mangrove forests. Biotrop. 30, 510–518.

FAO, 1985. Mangrove management in Thailand, Malaysia and Indonesia. FAO Environment Paper 4, Food and Agriculture Organization of the United Nations, Rome.

FAO, 1994. Mangrove forest management guidelines. FAO Forestry Paper 117, Food and Agriculture Organization of the United Nations, Rome.

Farber, S., 1987. The value of coastal wetlands for protection of property against hurricane wind damage. J. Environ. Econ. Manage. 14, 143–151.

Farnsworth, E.J., Ellison, A.M., 1997. The global conservation status of mangroves. Ambio 26, 328–334.

Festinger, L.A., 1957. Theory of Cognitive Dissonance. Row, Peterson, New York.

Field, C.D. (Ed.), 1996. Restoration of Mangrove Ecosystems. International Society of Mangrove Ecosystems and ITTO, Okinawa, Japan.

Field, C.D., 1998. Rehabilitation of mangrove ecosystems: an overview. Mar. Poll. Bull. 37, 383–392.

Field, C.D., Dartnall, A.J. (Eds.), 1987. Mangrove Ecosystems of Asia and the Pacific: Status, Exploitation and Management. Australian Development Assistance Bureau and Australian Committee for Mangrove Research, Townsville.

Fong, F.W., 1992. Perspectives for sustainable resource utilization and management of nipa vegetation. Econ. Bot. 46, 45–54.

Fosberg, F.R., 1971. Mangroves versus tidal waves. Biol. Conserv. 4, 38–39.

Fromard, F., Vega, C., Proisy, C., 2004. Half a century of dynamic coastal change affecting mangrove shorelines of French Guiana: a case study based on remote sensing data analyses and field surveys. Mar. Geol. 208, 265–280.

Furukawa, K., Wolanski, E., Mueller, H., 1997. Currents and sediment transport in mangrove forests. Estuar. Coast. Shelf Sci. 44, 301–310.

Gao, J., 1998. A hybrid method toward accurate mapping of mangroves in a marginal habitat from SPOT multispectral data. Int. J. Remote Sens. 19, 1887–1899.

Gattuso, J.P., Frankignoulle, M., Wollast, R., 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. A. Rev. Ecol. Syst. 29, 405–434.

Ghimire, S.K., McKey, D., Aumeeruddy-Thomas, Y., 2004. Heterogeneity in ethnoecological knowledge and management of medicinal plants in the Himalayas of Nepal: Implications for conservation. Ecol. Soc. 9 (3) art 6.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Glaser, M., 2003. Interrelations between mangrove ecosystem, local economy and social sustainability in Caete Estuary, North Brazil. Wetland Ecol. Manage. 11, 265–272.

Glaser, M., Oliveira, R., 2004. Prospects for the co-management of mangrove ecosystems on the North Brazilian coast: whose rights, whose duties and whose priorities? Nat. Resour. Forum 28, 224–233.

Gong, W.K., Ong, J.E., 1995. The use of demographic studies in mangrove silviculture. Hydrobiologia 295, 255–261.

Gong, W.K., Ong, J.E., Wong, C.H., Dhanarajan, G., 1980. Productivity of mangrove trees and its significance in a managed mangrove ecosystem in Malaysia. Mangrove Environmental Research and Management, University of Malaysia, Kuala Lumpur and UNESCO.

Green, E.P., Mumby, P.J., Alaisdair, E.J., Clark, C.D., Ellis, A.C., 1997. Estimating leaf area index of mangroves from satellite data. Aquat. Bot. 58, 11–19.

Green, E.P., Clark, C.D., Mumby, P.J., Edwards, A.J., Ellis, A.C., 1998. Remote sensing techniques for mangrove mapping. Int. J. Remote Sens. 19, 935–956.

Hamilton, L.S., Snedaker, S.C. (Eds.), 1984. Handbook for Mangrove Area Management. IUCN/Unesco/UNEP. East-West Centre, Honolulu, Hawaii.

Hamilton, L.S., Dixon, J.A., Miller, G.O., 1989. Mangrove forests: an undervalued resource of the land and of the sea. In: Borgese, E.M., Ginsburg, N., Morgan, J.R. (Eds.), Ocean Yearbook 8. University of Chicago Press, Chicago, pp. 254–288.

Harakunarak, A., Aksornkoae, S., July 2005. Life-saving belts: post-tsunami reassessment of mangrove ecosystem values and management in Thailand. Trop. Coasts 2005, 48–55.

Hauff, R.D., Ewel, K.C., Jack, J., 2006. Tracking human disturbance in mangroves: estimating harvest rates on a Micronesian island. Wet. Ecol. Manage 14, 95–105.

Hernández Cornejo, R., Koedam, N., Ruiz Luna, A., Troell, M., Dahdouh-Guebas, F., 2005. Remote sensing and ethnobotanical assessment of the mangrove forest changes in the Navachiste-San Ignacio-Macapule lagoon complex, Sinaloa, Mexico. Ecol. Soc. 10 (1) art 16.

Hong, P.N. (Ed.), 2006. The Role of Mangrove and Coral Reef Ecosystems in Natural Disaster Mitigation and Coastal Life Improvement. The World Conservation Union, and Mangrove Ecosystem Research Division, Viet Nam National University, Hanoi. 386 pp.

Hoq, M.E., 2007. An analysis of fisheries exploitation and management practices in the Sundarbans mangrove ecosystem, Bangladesh. Ocean Coast. Manage. 50, 411–427.

Hussain, M.Z., 1995. Silviculture of mangroves. Unasylva 181 (46), 36–42.

Hussain, M.Z., Ahmed, I., 1994. Management of forest resources. In: Hussain, M.Z., Acharya, G. (Eds.), Mangroves of the Sundarbans, vol. 2. IUCN, Bangladesh.

IUCN, 2005. Economic value of mangroves: a case study to value the shoreline protection, goods and services provided by healthy mangroves. IUCN Tsunami Response, 1–2.

Jayatissa, L.P., Hettiarachchi, S., Dahdouh-Guebas, F., 2006. An attempt to recover economic losses from decadal changes in two lagoon systems of Sri Lanka through a newly patented mangrove product. Environ. Dev. Sustain. 8, 585–595.

Jensen, J.R., Lin, H., Yang, Y., Ramsey, E., Davis, B.A., Thoemke, C.W., 1991. The measurement of mangrove characteristics in Southwest Florida using SPOT multispectral data. Geocarto Int. 2, 13–21.

Kairo, J.G., Dahdouh-Guebas, F., Bosire, J., Koedam, N., 2001. Restoration and management of mangrove systems—a lesson for and from the East African region. S. Afr. J. Bot. 67, 383–389.

Kairo, J.G., Dahdouh-Guebas, F., Gwaba, P.O., Ochieng, C., Koedam, N., 2002. Regeneration status of mangrove forests in Mida Creek, Kenya: a compromised or secured future? Ambio 31, 562–568.

Kaly, U.L., Jones, G.P., 1998. Mangrove restoration: a potential tool for coastal management in tropical developing countries. Ambio 27, 656–661.

Kaplowitz, M.D., 2001. Assessing mangrove products and services at the local level: the use of focus groups and individual interviews. Landsc. Urban Plann. 56, 53–60.

Kathiresan, K., 2003. How do mangrove forests induce sedimentation? Revista Biol. Trop. 51, 355–360.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. Adv. Mar. Biol. 40, 81–251.

Kathiresan, K., Rajendran, N., 2005. Coastal mangrove forests mitigated tsunami. Estuar. Coast. Shelf Sci. 65, 601–606.

Kautsky, N., Rönnbäck, P., Tedengren, M., Troell, M., 2000. Ecosystem perspectives on management of disease in shrimp pond farming. Aquaculture 191 (1–3), 145–161.

Kerr, A.M., Baird, A.H., 2007. Natural barriers to natural disasters. BioSci. 57, 102–103.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Kovacs, J.M., 1999. Assessing mangrove use at the local scale. Landsc. Urban Plann. 43, 201–208.

Kovacs, J.M., 2000. Perceptions of environmental change in a tropical coastal wetland. Land Degradr. Dev. 11, 209–220.

Kovacs, J.M., Wang, J., Blanco-Correa, M., 2001a. Mapping mangrove disturbances using multi-date Landsat TM imagery. Environ. Manage. 27, 763–776.

Kovacs, J.M., Blanco-Correa, M., Flores-Verdugo, F., 2001b. A logistic regression model of hurricane impacts in a mangrove forest of the Mexican Pacific. J. Coast. Res. 17, 30–37.

Kovacs, J.M., Flores-Verdugo, F., Wang, J., Aspden, L.P., 2004a. Estimating leaf area index of a degraded mangrove forest using high spatial resolution satellite data. Aquat. Bot. 80, 13–22.

Kovacs, J.M., Malczewski, J., Flores-Verdugo, F., 2004b. Examining local ecological knowledge of hurricane impacts in a mangrove forest using an Analytical Hierarchy Process (AHP) approach. J. Coast. Res. 20, 792–800.

Kovacs, J.M., Wang, J., Flores-Verdugo, F., 2005. Mapping mangrove leaf area index at the species level using IKONOS and LAI-2000 sensors. Estuar. Coast Shelf Sci. 62, 377–384.

Kovacs, J.M., Vandenberg, C.V., Flores-Verdugo, F., 2006. Assessing fine beam RADARSAT-1 backscatter from a white mangrove (*Laguncularia racemosa* (Gaertner)) canopy. Wetland Ecol. Manage. 14, 401–408.

Kovacs, J.M., Vandenberg, C.V., Wang, J., Flores-Verdugo, F., 2008. The use of multipolarized spaceborne SAR backscatter for monitoring the health of a degraded mangrove forest. J. Coast. Res. 24, 248–254.

Krause, G., Bock, M., Weiers, St., Braun, G., 2004. Mapping land-cover and mangrove structures with remote sensing techniques—a contribution to a synoptic GIS in support of coastal management in north Brazil. Environ. Manage. 34, 429–440.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Kühlmann, D.H.H., 1988. The sensitivity of coral reefs to environmental pollution. Ambio 17, 13–21.

Kunstadter, P., Bird, E.C.F., Sabhasri, S. (Eds.), 1986. Man in the Mangroves. United Nations University, Tokyo.

Kushwaha, S.P.S., Dwivedi, R.S., Rao, B.R.M., 2000. Evaluation of various digital image processing techniques for detection of coastal wetlands using ERS-1 SAR data. Int. J. Remote Sens. 21, 565–579.

Lacerda, L.D. (Ed.), 1993. Conservation and sustainable utilization of mangrove forests in Latin America and African regions (Part 1: Latin America). Mangrove Ecosystem Technical Reports 2, International Society for Mangrove Ecosystems and International Tropical Timber Organization, Tokyo.

Lacerda, L.D. (Ed.), 2002. Mangrove Ecosystems: Function and Management. Springer, New York.

Lacerda, L.D., Conde, J.E., Bacon, P.R., Alarcon, C., D'Croz, L., Kjerfve, B., Polania, J., Vanucci, M., 1993. Mangrove ecosystems in Latin America and the Caribbean: a summary. In: Lacerda, L.D. (Ed.), Conservation and Sustainable Utilization of Mangrove Forests in Latin America and African regions (Part 1: Latin America). Mangrove Ecosystem Technical Reports 2, International Society for Mangrove Ecosystems and International Tropical Timber Organization, Tokyo.

Lacerda, L.D., Conde, J.E., Kjerfve, B., Alvarez-Leon, R., Alarcon, C., Plania, J., 2002. American mangroves. In: Lacerda, L.D. (Ed.), Mangrove Ecosystems: Function and Management. Springer, New York, pp. 1–61.

Lal, P.N., 1990. Conservation or conversion of mangroves in Fiji: An ecological economic analysis.Occasional Paper No. 11, East-West Environment and Policy Institute, Honolulu, 108 pp.

Lal, P.N., 2002. Integrated and adaptive mangrove management framework—an action oriented option for the new millennium. In: Lacerda, L.D. (Ed.), Mangrove Ecosystems: Function and Management. Springer-Verlag, Berlin, pp. 235–256.

Lee, S.Y., 2004. Relationship between mangrove abundance and tropical prawn production: a re-evaluation. Mar. Biol. 145, 943–949.

Lewis, R.R., 1992. Coastal habitat restoration as a fishery management tool. In: Stroud, R.H. (Ed.), Stemming the Tide of Coastal Fish Habitat Loss. National Coalition for Marine Conservation, Inc, Savannah, pp. 169–173.

Lewis, R.R., 2000. Ecological based goal setting in mangrove forest and tidal marsh restoration. Ecol. Eng. 15, 191–198.

Lewis, R.R., 2005. Ecological engineering for successful management and restoration of mangrove forests. Ecol. Eng. 24, 403–418.

Liu, P.L.-F., Lynett, P., Fernando, H., Jaffe, B.E., Fritz, H., Higman, B., Morton, R., Goff, J., Synolakis, C., 2005. Observations by the international tsunami survey team in Sri Lanka. Science 308, 1595.

Long, B.G., Skewes, T.D., 1996. A technique for mapping mangroves with Landsat TM satellite data and geographic information system. Estuar. Coast. Shelf Sci. 43, 373–381.

Lopez-Hoffman, L., Monroe, I.E., Narvaez, E., Martinez-Ramos, M., Ackerly, D.D., 2006. Sustainability of mangrove harvesting: how do harvesters' perceptions differ from ecological analysis? Ecol. Soc. 11 (2) art 14.

Macintosh, D.J., 1982. Fisheries and aquaculture significance of mangrove swamps, with special reference to the Indo-West Pacific region. In: Muir, J.F., Roberts, R.J. (Eds.), Recent Advances in Aquaculture. Croom Helm, England, pp. 4–85.

Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. Adv. Mar. Biol. 6, 73–270.

Magalhaes, A., da Costa, R.M., da Silva, R., Cajueiro, L., Pereira, C., 2007. The role of women in the mangrove crab (*Ucides cordatus, Ocypodidae*) production process in North Brazil (Amazon region, Pará). Ecol. Econ. 61, 559–565.

Mainoya, J.R., Mesaki, S., Banyikwa, F.F., 1986. The distribution and socio-economic aspects of mangrove forests in Tanzania. In: Kunstadter, P., Bird, E.C.F., Sabhasri, S. (Eds.), Man in the Mangroves. United Nations University, Tokyo, pp. 87–95.

Massel, S.R., Furukawa, K., Brinkman, R.M., 1999. Surface wave propagation in mangrove forests. Fluid Dyn. Res. 24, 219–249.

Mastaller, M., 1997. Mangroves, the Forgotten Forest between Land and Sea. Tropical Press Sdn. Bhd, Kuala Lumpur, Malaysia, 200.

Matthes, H., Kapetsky, J.M., 1988. Worldwide compendium of mangrove-associated aquatic species of economic importance. FAO Fishery Circular No. 814, FAO, Rome.

Mazda, Y., Magi, M., Kogo, M., Hong, P.N., 1997. Mangroves as a coastal protection from waves in the Tong King Delta, Vietnam. Mangr. Salt Marsh. 1, 127–135.

Meltzoff, S.K., LiPuma, E., 1986. The social and political economy of coastal zone management: Shrimp mariculture in Ecuador. Coast. Zone Manage. J. 14, 349–380.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well Being: Synthesis. World Resources Institute, Washington, DC.

Moberg, F., Rönnbäck, P., 2003. Ecosystem services of the tropical seascape: Interactions, substitutions, and restoration. Ocean Coast. Manage. 46, 27–46.

Moller, H., Berkes, F., 2004. Combining science and traditional ecological knowledge: monitoring populations for co-management. Ecol. Soc. 9 (3) art 2.

Morton, J.F., 1965. Can the red mangrove provide food, feed and fertilizer? Econ. Bot. 19, 113–123.

Mougin, E., Proisy, C., Marty, G., Fromard, F., Puig, H., Betoulle, J.L., Rudant, J.P., 1999. Multifrequency and multipolarization radar backscattering from mangrove forests. IEEE Trans. Geosci. Remote Sens. 37, 94–102.

Muttitanon, W., Tripathi, N.K., 2005. Land use/land cover changes in the coastal zone of Ban Don Bay, Thailand using Landsat TM data. Int. J. Remote Sens. 26, 231–2323.

Nagelkerken, I., van der Velde, G., 2004. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. Mar. Ecol. Progr. Ser. 274, 153–159.

Nagelkerken, I., Roberts, C.M., van der Velde, G., Dorenbosch, M., van Riel, M.C., Cocheret de la Moriniere, E., Nienhuis, P.H., 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Mar. Ecol. Progr. Ser. 244, 299–305.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., Cocheret de la Moriniere, E., van der Velde, G., 2000. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar. Ecol. Progr. Ser. 202, 175–192.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Naylor, R.L., Drew, M., 1998. Valuing mangrove resources in Kosrae, Micronesia. Environ. Dev. Econ. 3, 471–490.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M., Clay, J., Folke, C., Lubchenco, J., Mooney, H., Troell, M., 2000. Effect of aquaculture on world fish supplies. Nature 405, 1017–1024.

Naylor, R.L., Bonine, K.B., Ewel, K.C., Waguk, E., 2002. Migration, markets and mangrove resource use on Kosrae, Federated States of Micronesia. Ambio 31, 340–350.

Nickerson, D.J., 1999. Trade-offs of mangrove area development in the Philippines. Ecol. Econ. 28, 279–298.

Nurkin, B., 1994. Degradation of mangrove forests in South Sulawesi, Indonesia. Hydrobiologia 285, 271–276.

Ogden, J.C., 1997. Ecosystem interactions in the tropical coastal seascape. In: Birkeland, C. (Ed.), Life and Death of Coral Reefs. Chapman & Hall, London, pp. 288–297.

Omodei-Zorini, L., Contini, C., Jiddawi, N., Ochiewo, J., Shunula, J., Cannicci, S., 2004. Participatory appraisal for potential community-based mangrove management in East Africa. Wetland Ecol. Manage. 12, 87–102.

Ong, J.E., 1993. Mangroves—a carbon source and sink. Chemosph. 27, 1097–1107.

Ong, J.E., 1995. The ecology of mangrove conservation and management. Hydrobiologia 295, 343–351.

Othman, M.A., 1994. Value of mangroves in coastal protection. Hydrobiologia 285, 277–282.

Overdorf, J., Unmacht, E., 2005. Why save the forests? Fear of big waves is no reason to plant mangroves. Newsweek CXLV (7) 49 (Feb. 14).

Pauly, D., Ingles, J., 1986. The relationship between shrimp yields and intertidal (mangrove) areas: a reassessment. In: IOC/FAO Workshop on Recruitment in Tropical Coastal Demersal Communities. IOC, UNESCO, Paris, pp. 227–284.

Pinzon, Z.S., Ewel, K.C., Putz, F.E., 2003. Gap formation and forest regeneration in a Micronesian mangrove forest. J. Trop. Ecol. 19, 143–153.

Primavera, J.H., 1993. A critical review of shrimp pond culture in the Philippines. Rev. Fish. Sci. 1, 151–201.

Primavera, J.H., 1995. Mangroves and brackish water pond culture in the Philippines. Hydrobiologia 295, 303–309.

Primavera, J.H., 1998a. Tropical shrimp farming and its sustainability. In: de Silva, S. (Ed.), Tropical Mariculture. Academic Press, London, pp. 257–289.

Primavera, J.H., 1998b. Mangroves as nurseries: shrimp populations in mangrove and non-mangrove habitats. Estuar. Coast. Shelf Sci. 46, 457–464.

Primavera, J.H., 2000a. Development and conservation of Philippine mangroves: institutional issues. Ecol. Econ. 35, 91–106.

Primavera, J.H., 2000b. Integrated mangrove-aquaculture systems in Asia. Integr. Coast. Zone Manage. Autumn ed. 121–130.

Primavera, J.H., 2005. Mangroves, fishponds, and the quest for sustainability. Science 310, 57–59.

Primavera, J.H., Agbayani, R.F., 1997. Comparative strategies in community-based mangrove rehabilitation programmes in the Philippines. In: Hong, P.N., Ishwaran, N., San, H.T., Tri, N.H., Tuan, M.S. (Eds.), Proceedings of Ecotone V, Community Participation in Conservation, Sustainable Use and Rehabilitation of Mangroves in Southeast Asia, UNESCO, Japanese Man and the Biosphere National Committee and Mangrove Ecosystem Research Centre, Vietnam. pp. 229–243.

Primavera, J.H., de la Pena, L., 2000. The yellow mangrove: its ethnobotany, history of maritime collection, and needed rehabilitation in the central and southern Philippines. Philipp. Quart. Cult. Soc. 28, 464–475.

Primavera, J.H., Lebata, J.H., Altamirano, J., Gustilo, L., 2002. Collection of the clam *Anodontia edentula* in mangrove habitats in Panay and Guimaras, Central Philippines. Wetland Ecol. Manage. 10, 363–370.

Primavera, J.H., Sadaba, R.B., Lebata, M.J.H.L., Altamirano, J.P., 2004. Handbook of Mangroves in the Philippines—Panay. SEAFDEC Aquaculture Department (Philippines) and UNESCO Man and the Biosphere ASPACO Project, 106 pp.

Primavera, J.H., Altamirano, J.P., Lebata, M.J.H.L., de los Reyes Jr., A.A., Pitogo, C.L., 2007. Mangroves and shrimp pond culture effluents in Aklan, Panay Is., central Philippines. Bull. Mar. Sci. 80, 795–804.

Putz, F.E., Chan, H.T., 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. For. Ecol. Manage. 17, 211–230.

Ramsey, E., Jensen, J.R., 1996. Remote sensing of mangrove wetlands: relating canopy spectra to site-specific data. Photogramm. Eng. Remote Sens. 62, 939–948.

Rasolofo, M.V., 1997. Use of mangroves by traditional fishermen in Madagascar. Mangr. Salt Marsh. 1, 243–253.

Rasolofoharinoro, M., Blasco, F., Bellan, M.F., Aizpuru, M., Gauquelin, T., Denis, J., 1998. A remote sensing based methodology for mangrove studies in Madagascar. Int. J. Remote Sens. 19, 1873–1886.

Rist, S., Dahdouh-Guebas, F., 2006. Ethnosciences—a step towards the integration of scientific and traditional forms of knowledge in the management of natural resources for the future. Env. Dev. Sustain. 8, 467–493.

Rivera-Monroy, V.H., Twilley, R.R., Boustany, R.G., Day, J.W., Veraherrera, F., Ramirez, M.D., 1995. Direct denitrification in mangrove sediments in Terminos Lagoon, Mexico. Mar. Ecol. Progr. Ser. 126, 97–109.

Robertson, A.I., Duke, N.C., 1990a. Mangrove fish communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Mar. Biol. 104, 369–379.

Robertson, A.I., Duke, N.C., 1990b. Recruitment, growth and residence time of fishes in a tropical Australian mangrove system. Estuar. coast. Shelf Sci. 31, 723–743.

Robertson, A.I., Phillips, M.J., 1995. Mangroves as filters of shrimp pond effluents: predictions and biogeochemical research needs. Hydrobiologia 295, 311–321.

Rönnbäck, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol. Econ. 29, 235–252.

Rönnbäck, P., Troell, M., Primavera, J.H., Kautsky, N., 1999. Distribution pattern of shrimp and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao Mangroves, Philippines. Estuar. Coast. Shelf Sci. 48, 223–234.

Rönnbäck, P., Macia, A., Almqvist, G., Schultz, L., Troell, M., 2002. Do penaeid shrimps have a preference for mangrove habitats? Distribution pattern analysis on Inhaca Island, Mozambique. Est. Coast. Shelf Sci. 55, 427–436.

Rönnbäck, P., Troell, M., Zetterström, T., Babu, D.E., 2003. Mangrove dependence and socio-economic concerns in shrimp hatcheries of Andhra Pradesh, India. Environ. Conserv. 30, 344–352.

Rönnbäck, P., Crona, B., Ingwall, L., 2007a. The return of ecosystem goods and services in replanted mangrove forests—perspectives from local communities in Gazi Bay, Kenya. Environ. Conserv. 34, 313–324.

Rönnbäck, P., Troell, M., Kautsky, N., Pihl, L., Söderqvist, T., Wennhage, H., 2007b. Ecosystem goods and services from temperate coastal habitats – identification, valuation and implications of ecosystem shifts. Ambio 36, 534–544.

Roy, S.D., Krishnan, P., 2005. Mangrove stands of Andamans vis-à-vis tsunami. Curr. Sci. 89, 1800–1804.

Ruitenbeek, H.J., 1994. Modeling economy-ecology linkages in mangroves: economic evidence for promoting conservation in Bintuni Bay, Indonesia. Ecol. Econ. 10, 233–247.

Saenger, P., 1996. Mangrove restoration in Australia: a case study of the Brisbane international airport. In: Field, C.D. (Ed.), Restoration of Mangrove Ecosystems. International Society for Mangrove Ecosystems, Okinawa, Japan, pp. 36–51.

Saenger, P., 2002. Mangrove Ecology, Silviculture and Conservation. Kluwer Academic Publishers/The Society for Mangrove Ecosystems/International Tropical Timber Organization, Dordrecht, The Netherlands/Okinawa, Japan.

Saenger, P., Siddiqi, N.A., 1993. Land from the sea: the mangrove afforestation program in Bangladesh. Ocean Coast. Manage. 20, 23–39.

Saenger, P., Hegerl, E.J., Davie, J.D.S., 1983. Global status of mangrove ecosystems. Environmentalist 3 (Suppl. 3), 88.

Saito, H., Bellan, M.F., Al-Habshi, A., Aizpuru, M., Blasco, F., 2003. Mangrove research and coastal ecosystem studies with SPOT-4 HRVIR and TERRA ASTER in the Arabian Gulf. Int. J. Remote Sens. 24, 4073–4092.

Sánchez, L.M., Ruedas, D., Gómez, B.C., 2001. Gastric antiulcer effect of *Rhizophora mangle* L. J. Ethnopharm. 77, 1–3.

Sangdee, P., 1986. Health and sanitation among mangrove dwellers in Thailand. In: Kunstadter, P., Bird, E.C.F., Sabhasri, S. (Eds.), Man in the Mangroves. United Nations University, Tokyo, pp. 44–49.

Sathirathai, S., Barbier, E.B., 2001. Valuing mangrove conservation in southern Thailand. Contemp. Econ. Policy 19, 109–122.

Semesi, A.K., 1998. Mangrove management and utilization in Eastern Africa. Ambio 27, 620–626.

Serafy, J.E., Araújo, R.J. (eds.), 2007. Proceedings of the 1st International Symposium on Mangroves as Fish Habitat. Bull. Mar. Sci. (special issue) 80, 451–935.

Siddall, S.E., Atchue, J.A., III, Murray, P.L., Jr., 1985. Mariculture development in mangroves: a case study of the Philippines, Panama and Ecuador. In: Clark, J.R. (Ed.) Coastal Resources Management: Development Case Studies. Renewable Resources Information Series, Coastal Management Pub. No. 3. Prepared for the National Park Service, U.S. Dept. of the Interior, and the U.S. Agency for International Development. Research Planning Institute, Columbia, South Carolina, USA.

Simard, M., De Grandi, G., Saatchi, S., Mayaux, P., 2002. Mapping tropical coastal vegetation using JERS-1 and ERS-1 radar data with a decision tree classifier. Int. J. Remote Sens. 23, 1461–1474.

Singh, H.R., Chong, V.C., Sasekumar, A., Lim, K.H., 1994. Value of mangroves as nursery and feeding grounds. In: Wilkinson, C.R., Suraphol, S., Chou, L.M. (Eds.), Proceedings of the Third ASEAN-Australia Symposium on Living Coastal Resources, vol. 1. Status Reviews, Chulalongkorn University, Bangkok, pp. 105–122.

Smith, A.H., Berkes, F., 1993. Community-based use of mangrove resources in St. Lucia. Int. J. Environ. Stud. 43, 123–131.

Spalding, M., Blasco, F., Field, C., 1997. World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa, Japan.

Staples, D.J., Vance, D.J., Heales, D.S., 1985. Habitat requirement of juvenile penaeid prawns. In: Rothlisberg, P.C., Hill, B.J., Staples, D.S. (Eds.), Second National Prawn Seminar. NSP2, Cleveland, Australia, pp. 47–54.

Stevenson, N.J., Lewis, R.R., Burbridge, P.R., 1999. Disused shrimp ponds and mangrove rehabilitation. In: Streever, W. (Ed.), An International Perspective on Wetland Rehabilitation. Kluwer Academic Publishers, Netherlands, pp. 277–297.

Stone, R., 2006. A rescue effort for tsunami-ravaged Mangrove forests. Science 314, 404–1404.

Stonich, S., Bailey, C., 2000. Resisting the blue revolution: contending coalitions surrounding industrial shrimp farming. Hum. Organiz. 59, 23–36.

Stonich, S., Vandergeest, P., 2001. Violence, environment, and industrial shrimp farming. In: Peluso, N.L., Watts, M. (Eds.), Violent Environments. Cornell University Press, Ithaca, New York, pp. 261–286.

Taylor, F.J., 1982. The utilization of mangrove areas in Thailand and Peninsular Malaysia. J. Southeast Asian Stud. 13, 1–8.

Thorhaug, A., 1990. Restoration of mangroves and seagrasses—economic benefits for fisheries and mariculture. In: Berger, J.J. (Ed.), Environmental Restoration: Science and Strategies for Restoring the Earth. Island Press, Washington DC, pp. 265–281.

Tobisson, E., Andersson, J., Ngazi, Z., Rydberg, L., Cederlöf, U., 1998. Tides, monsoons and seabed: Local knowledge and practice in Chwaka Bay. Zanzibar. Ambio 27, 677–685.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Tong, P.H.S., Auda, Y., Populus, J., Aizpuru, M., Al-Habshi, A., Blasco, F., 2004. Assessment from space of mangrove evolution in the Mekong Delta, in relation to extensive shrimp farming. Int. J. Remote Sens. 25, 4795–4812.

Turner, R.E., 1977. Intertidal vegetation and commercial yields of penaeid shrimp. T. Am. Fish. Soc. 106, 411–416.

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 Pollut. 64, 264–288.

Untawale, A.G., 1987. Exploitation of mangroves in India. In: Field, C.D., Dartnall, A.J. (Eds.), Mangrove Ecosystems of Asia and the Pacific: Status, Exploitation and Management. Australian Development Assistance Bureau and Australian Committee for Mangrove Research, Townsville, pp. 220–227.

Valiela, I., Bowen, J.L., York, J.K., 2001. Mangrove forests: one of the world's threatened major tropical environments. BioSci. 51, 807–815.

Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., Pendrey, R.C., 1996. How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia. Mar. Ecol. Prog. Ser. 131, 115–124.

Vandergeest, P., Flaherty, M., Miller, P., 1999. A political ecology of shrimp aquaculture in Thailand. Rural Sociol. 64, 573–596.

Vannucci, M., 2002. Indo-West pacific mangroves. In: Lacerda, L.D. (Ed.), Mangrove Ecosystems: Function and Management. Springer, New York, pp. 123–215.

Vayda, A.P., Walters, B.B., 1999. Against political ecology. Human Ecol. 27, 167–179.

Vayda, A.P., Walters, B.B., Setyawati, I., 2004. Doing and knowing: questions about studies of local knowledge. In: Bicker, A., Sillitoe, P., Pottier, J. (Eds.), Investigating Local Knowledge: New Directions, New Approaches. Ashgate, London, pp. 35–58.

Vedeld, P., Angelsen, A., Sjaastad, E., Berg, G.K., 2004. Counting on the environment: Forest incomes and the rural poor. Environmental Economics Series Paper No. 98, World Bank, Washington, DC.

Verheugt, W.J.M., Purwoko, A., Danielsen, F., Skov, H., Kadarisman, R., 1991. Integrating mangrove and swamp forests conservation with coastal lowland development: the Banyuasin Sembilang swamps case study, South Sumatra Province, Indonesia. Landsc. Urban Plann. 20, 85–94.

Walsh, G.E., 1977. Exploitation of mangal. In: Chapman, V.J. (Ed.), Wet Coastal Ecosystems. Elsevier Science, New York, pp. 347–362.

Walters, B.B., 1997. Human ecological questions for tropical restoration: experiences from planting native upland forest and coastal mangrove trees in the Philippines. For. Ecol. Manage. 99, 275–290.

Walters, B.B., 2000. Local mangrove planting in the Philippines: are fisherfolk and fishpond owners effective restorationists? Restor. Ecol. 8, 237–246.

Walters, B.B., 2003. People and mangroves in the Philippines: fifty years of coastal environmental change. Environ. Conserv. 30, 293–303.

Walters, B.B., 2004. Local management of mangrove forests: effective conservation or efficient resource exploitation? Hum. Ecol. 32, 177–195.

Walters, B.B., 2005a. Patterns of local wood use and cutting of Philippine mangrove forests. Econ. Bot. 59, 66–76.

Walters, B.B., 2005b. Ecological effects of small-scale cutting of Philippine mangrove forests. For. Ecol. Manage. 206, 331–348.

Walters, B.B., 2006. Mangrove forests and environmental security. In: Innes, J.I., Edwards, I.K, Wilford, D.J. (Eds.), Forests in the balance: linking tradition and technology. Abstracts, XXII IUFRO World Congress, Brisbane, Australia, August 8–13, 2005. Int. For. Rev. 7(5), 290.

Walters, B.B., Burt, M., 1991. Integrated management of common property fuelwood resources from natural and plantation forests. CANARI Communication No. 35, Caribbean Natural Resources Institute, St. Lucia. Paper presented at the IDRC Workshop on Common Property Resources, Winnipeg, Canada, September 1991.

Walters, B.B., Sabogal, C., Snook, L., de Almeida, E., 2005. Constraints and opportunities for better silviculture practice in tropical forestry: an interdisciplinary approach. For. Ecol. Manage. 209, 3–18.

Walton, M.E., LeVay, L., Lebata, J.H., Binas, J., Primavera, J.H., 2006a. Seasonal abundance, distribution and recruitment of mud crabs (*Scylla* spp.) in replanted mangroves. Estuar. Coast. Shelf Sci. 66, 493–500.

Walton, M.E., Samonte-Tan, G., Primavera, J.H., Edwards-Jones, G., Le Vay, L., 2006b. Are mangroves worth replanting? The direct economic benefits of a community-based reforestation project. Environ. Conserv. 33, 335–343.

Wang, L., Sousa, W.P., Gong, P., 2004a. Integration of object-based and pixel-based classification for mapping mangroves with IKONOS imagery. Int. J. Remote Sens. 25, 5655–5668.

Wang, L., Sousa, W.P., Gong, P., Biging, G.S., 2004b. Comparison of IKONOS and QuickBird images for mapping mangrove species on the Caribbean coast of Panama. Remote Sens. Environ. 91, 432–440.

Watson, J.G., 1928. Mangrove Forests of the Malay Peninsula. Malayan Forester, Record No. 6. Federated Malay States.

Webb, E.L., Evangelista, M.A., Robinson, J.A., 2000. Digital land-use classification using space-shuttle-acquired orbital photographs: a quantitative comparison with Landsat TM imagery of a coastal environment, Chanthaburi, Thailand. Photogramm. Eng. Remote Sens. 66, 1439–1449.

Weinstock, J.A., 1994. *Rhizophora* mangrove agroforestry. Econ. Bot. 48, 210–213.

Wells, S., Kapos, V., 2006. Coral reefs and mangroves: implications from the tsunami one year on. Oryx 40, 123–124.

Wilkie, M.L., Fortuna, S., 2003. Status and trends in mangrove area extent worldwide. Working Paper FRA 63, Forest Resources Division, Forestry Department, UN-Food and Agriculture Organization, 292 pp.

Williams, N., 2005. Tsunami insight to mangrove value. Curr. Biol. 15, R73–R173.

Williams, M.J., Coles, R., Primavera, J.H., 2007. A lesson from cyclone Larry: an untold story of the success of good coastal planning. Estuar. Coast. Shelf Sci. 71, 364–367.

Wolanski, E., 1995. Transport of sediment in mangrove swamps. Hydrobiologia 295, 31–42.

Yanez-Arancibia, A., Lara-Dominguez, A.L., Day Jr., J.W., 1993. Interactions between mangrove and seagrass habitats mediated by estuarine nekton assemblages: coupling of primary and secondary productivity. Hydrobiologia 264, 1–12.

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Review

Threats to mangroves from climate change and adaptation options: A review

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Abstract

Mangrove ecosystems are threatened by climate change. We review the state of knowledge of mangrove vulnerability and responses to predicted climate change and consider adaptation options. Based on available evidence, of all the climate change outcomes, relative sea-level rise may be the greatest threat to mangroves. Most mangrove sediment surface elevations are not keeping pace with sea-level rise, although longer term studies from a larger number of regions are needed. Rising sea-level will have the greatest impact on mangroves experiencing net lowering in sediment elevation, where there is limited area for landward migration. The Pacific Islands mangroves have been demonstrated to be at high risk of substantial reductions. There is less certainty over other climate change outcomes and mangrove responses. More research is needed on assessment methods and standard indicators of change in response to effects from climate change, while regional monitoring networks are needed to observe these responses to enable educated adaptation. Adaptation measures can offset anticipated mangrove losses and improve resistance and resilience to climate change. Coastal planning can adapt to facilitate mangrove migration with sea-level rise. Management of activities within the catchment that affect long-term trends in the mangrove sediment elevation, better management of other stressors on mangroves, rehabilitation of degraded mangrove areas, and increases in systems of strategically designed protected area networks that include mangroves and functionally linked ecosystems through representation, replication and refugia, are additional adaptation options.

Keywords: Adaptation; Climate change; Mangrove; Mitigation; Sea-level rise

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1. Introduction

Climate change components that affect mangroves include changes in sea-level, high water events, storminess, precipitation, temperature, atmospheric CO_2 concentration, ocean circulation patterns, health of functionally linked neighboring ecosystems, as well as human responses to climate change. Of all the outcomes from changes in the atmosphere's composition and alterations to land surfaces, relative sea-level rise may be the greatest threat (Field, 1995; Lovelock and Ellison, 2007). Although, to date, it has likely been a smaller threat than anthropogenic activities such as conversion for aquaculture and filling (IUCN, 1989; Primavera, 1997; Valiela et al., 2001; Alongi, 2002; Duke et al., 2007), relative sea-level rise is a substantial cause of recent and predicted future reductions in the area and health of mangroves and other tidal wetlands (IUCN, 1989; Ellison and Stoddart, 1991; Nichols et al., 1999; Ellison, 2000; Cahoon and Hensel, 2006; McLeod and Salm, 2006; Gilman et al., 2006, 2007a,b).

Mangroves perform valued regional and site-specific functions (e.g., Lewis, 1992; Ewel et al., 1998; Walters et al., 2008). Reduced mangrove area and health will increase the threat to human safety and shoreline development from coastal hazards such as erosion, flooding, storm waves and surges, and tsunami, as most recently observed following the 2004 Indian Ocean tsunami (Danielsen et al., 2005; Kathiresan and Rajendran, 2005; Dahdouh-Guebas et al., 2005a,b, 2006). Mangrove loss will also reduce coastal water quality, reduce biodiversity, eliminate fish and crustacean nursery habitat, adversely affect adjacent coastal habitats, and eliminate a major resource for human communities that rely on mangroves for numerous products and services (Ewel et al., 1998; Mumby et al., 2004; Nagelkerken et al., 2008; Walters et al., 2008). Mangrove destruction can also release large quantities of stored carbon and exacerbate global warming and other climate change trends (Ramsar Secretariat, 2001; Kristensen et al., 2008). The annual economic values of mangroves, estimated by the cost of the products and services they provide, have been estimated to be USD 200,000–900,000 ha^{-1} (Wells et al., 2006). The value of Malaysian mangroves just for storm protection and flood control has been estimated at USD 300,000 km^{-1} of coastline, which is based on the cost of replacing the mangroves with rock walls (Ramsar Secretariat, 2001). The mangroves of Moreton Bay, Australia, were valued in 1988 at USD 4850 ha^{-1} based only on the catch of marketable fish (Ramsar Secretariat, 2001). Mangroves can also be provided with an economic value based on the cost to replace the products and services that they provide, or the cost to restore or enhance mangroves that have been eliminated or degraded. The range of reported costs for mangrove restoration is USD 225–216,000 ha^{-1}, not including the cost of the land (Lewis, 2005). In Thailand, restoring mangroves is costing USD 946 ha^{-1} while the cost for protecting existing mangroves is only USD 189 ha^{-1} (Ramsar Secretariat, 2001).

Accurate predictions of changes to coastal ecosystem area and health, including in response to projected relative sea-level rise and other climate change outcomes, enable site planning with sufficient lead time to minimize and offset anticipated losses (Titus, 1991; Mullane and Suzuki, 1997; Hansen and Biringer, 2003; Gilman et al., 2006, 2007a; Berger et al., 2008). We review the state of understanding of the effects of projected climate change on mangrove ecosystems, including the state of knowledge for assessing mangrove resistance and resilience to relative sea-level rise. Resistance is used here to refer to a mangrove's ability to keep pace with rising sea-level without alteration to its functions, processes and structure (Odum, 1989; Bennett et al., 2005). Resilience refers to the capacity of a mangrove to naturally migrate landward in response to rising sea-level, such that the mangrove ecosystem absorbs and reorganizes from the effects of the stress to maintain its functions, processes and structure (Carpenter et al., 2001; Nystrom and Folke, 2001). We then identify adaptation options to avoid and minimize adverse outcomes from predicted mangrove responses to projected climate change.

2. Climate change threats

2.1. Sea-level rise

Global sea-level rise is one of the more certain outcomes of global warming, it is already likely taking place (12–22 cm occurred during the 20th century), and several climate models project an accelerated rate of rise over coming decades (Cazenave and Nerem, 2004; Church et al., 2001, 2004a; Holgate and Woodworth, 2004; Thomas et al., 2004; Church and White, 2006; Solomon et al., 2007). The range of projections for global sea-level rise from 1980 to 1999 to the end of the 21st century (2090–2099) is 0.18–0.59 m (Solomon et al., 2007). Recent findings on global acceleration in sea-level rise indicate that upper projections are likely to occur (Church and White, 2006).

'Relative sea-level change', the change in sea-level relative to the local land as measured at a tide gauge, is a combination of the change in eustatic (globally averaged) sea-level and regional and local factors. The former is the change in sea-level relative to a fixed Earth coordinate system, which, over human time scales, is due primarily to thermal expansion of seawater and the transfer of ice from glaciers, ice sheets and ice caps to water in the oceans (Church et al., 2001). The latter is the result of vertical motion of the land from tectonic movement, the glacio- or hydro-isostatic response of the Earth's crust to changes in the weight of overlying ice or water, coastal subsidence such as due to extraction of subsurface groundwater or oil, geographical variation in thermal expansion, and for shorter time scales over years and shorter, meteorological and oceanographic factors (Church et al., 2001). The rate of change of relative sea-level as measured at a tide gauge may differ substantially from the relative sea-level rate of change occurring in coastal wetlands due to changing elevation of the wetland sediment surface. Additional variability might be caused by differences in local tectonic processes, coastal subsidence, sediment budgets, and meteorological and oceanographic factors between the section of coastline where the coastal wetland is situated and a tide gauge, especially when the tide gauge is distant from the wetland.

2.1.1. Mangrove vulnerability to sea-level rise

Mangrove systems do not keep pace with changing sea-level when the rate of change in elevation of the mangrove sediment surface is exceeded by the rate of change in relative sea-level. There are several interconnected surface and subsurface processes that influence the elevation of mangroves' sediment surface (Table 1). Mangroves of low relief islands in carbonate settings that lack rivers were thought to be the most sensitive to sea-level rise, owing to their sediment-deficit environments (Thom, 1984; Ellison and Stoddart, 1991; Woodroffe, 1987, 1995, 2002). However, recent studies have shown that subsurface controls on mangrove sediment elevation can offset high or low sedimentation rates (Cahoon et al., 2006; Cahoon and Hensel, 2006), such that sedimentation rates alone provide a poor indicator of vulnerability to rising sea-level.

The surface elevation table-marker horizon (SET-MH) method (Boumans and Day, 1993; Cahoon and Lynch, 1997; Cahoon et al., 2002; Krauss et al., 2003; Rogers et al., 2005a,b; Cahoon and Hensel, 2006; McKee et al., 2007) and stakes inserted through the organic peat layer to reach consolidated substrate (Gilman et al., 2007b) have been used to measure trends in wetland sediment elevation and determine how sea-

Table 1
Processes known to control the elevation of mangrove sediment surfaces

Process	Influence on mangrove sediment surface elevation
Sediment accretion and erosion	Sediment accretion and erosion are determined by a mangrove's geomorphic setting, which affects the sources of sediment, sediment composition, and method of delivery (Furukawa and Wolanski, 1996; Furukawa et al., 1997; Woodroffe, 1990, 2002). Fine sediment particles are carried in suspension into mangrove systems from coastal waters during tidal inundation, form large flocs (cohesive clay and fine silt), which settle in the forest during slack high tide as the friction caused by the high mangrove vegetation density slows tidal currents. Wrack or plant litter on the soil surface can also trap mineral sediment, and contribute to vertical accretion (Cahoon et al., 2006). Water currents during ebb tides are too low to re-entrain the sediment. Thus, the mangrove structure causes sediment accumulation (Furukawa and Wolanski, 1996). Storms and extreme high water events can alter the mangrove sediment elevation through soil erosion and deposition (Cahoon et al., 2003, 2006). Sedimentation varies by mangrove species and their root type (Furukawa and Wolanski, 1996; Krauss et al., 2003).
Biotic contributions	Biotic contributions to soil elevation vary from low (allochthonous mineral soils) to very high (autochthonous peat soils), where surface processes include the accumulation of decaying organic matter such as leaf litter, and the formation of living benthic microbial, algal or root mats (Woodroffe, 1992, 2002; Cahoon et al., 2006). The accumulation of leaf litter is controlled by aboveground production, consumption by detrivores, microbial decomposition and tidal flushing (Middleton and McKee, 2001; Cahoon et al., 2006).
Belowground primary production	When belowground root growth exceeds root decomposition, soil organic matter accumulates, causing a net increase in soil volume and contributes to a rise in sediment elevation. Root growth, or the lack thereof, has been shown to be a substantial control on mangrove soil elevation at some sites (Cahoon et al., 2003, 2006; Cahoon and Hensel, 2006; McKee et al., 2007). In particular, mangroves in carbonate settings, such as on low oceanic islands remote from continental sources of sediment, have autochthonous soil, composed primarily of mangrove roots, where belowground primary productivity and organic matter accumulation are primary controls on sediment elevation (Cahoon et al., 2006; McKee et al., 2007).
Autocompaction	Autocompaction, the lowering of the sediment surface and reduction in sediment volume, is caused by the oxidation (decomposition) and compression of organic material, and inorganic processes, including rearrangement of the mineral architecture, silica solution, clay dehydration and other diagenetic processes (Pizzuto and Schwendt, 1997; Cahoon et al., 1999; Allen, 2000; Woodroffe, 2002; Cahoon and Hensel, 2006). Autocompaction is understood to decrease asymptotically with the age of the mangrove (Woodroffe, 2002). Mangroves suffering mass tree mortality, caused by storms or other acute sources of stress, at sites with substrate composed primarily of peat or organic mud, are susceptible to substantial lowering in elevation of their sediment surface through peat collapse and soil compression (e.g., Cahoon et al., 2003).
Fluctuations in water table levels and pore water storage	Hydrology directly affects wetland elevation through processes of compression and dilation storage (Cahoon et al., 2006). The more water that is incorporated into the sediment below the water table, referred to as 'dilation storage' or 'shrink–swell', the more the sediment dilates, increasing sediment volume, increasing the elevation of the wetland sediment surface (Cahoon et al., 2006). The amount of dilation storage and degree of change in elevation of the sediment surface varies with soil type. Changes in groundwater inputs, such as from long-term changes in precipitation levels resulting from climate change, would result in a long-term change in mangrove elevation. Short-term cyclical influences include variability in precipitation and tidal range. Research conducted to date has demonstrated the short-term effects of groundwater recharge on mangrove elevation (Rogers et al., 2005a; Whelan et al., 2005). Research is lacking to demonstrate effects of long-term trends in changes in groundwater inputs.

level relative to the wetland sediment surface is changing. There have been observations of disparate trends in sediment elevation within an individual mangrove (Krauss et al., 2003; Rogers et al., 2005b; McKee et al., 2007). This highlights the importance of designing sampling methods to observe trends in change in surface elevation to adequately characterize a mangrove site. Furthermore, there can be large and significant differences between trends in mangrove sediment accretion and sediment elevation (Krauss et al., 2003; Rogers et al., 2005a; Whelan et al., 2005; Cahoon et al., 2006): Subsurface processes, in some cases in the deepest soil horizon, have been found to be primary controlling factors of elevation change (Whelan et al., 2005; Cahoon and Hensel, 2006). Therefore, sediment elevation monitoring needs to account for subsurface processes through the entire soil profile.

The understanding of how surface and subsurface processes control mangrove sediment surface elevation, and feedback mechanisms resulting from changes in relative sea-level, is poor. There are likely several feedback mechanisms, where processes that control the mangrove sediment elevation interact with changes in sea-level. Relatively short-term observations, over periods of a few years, documented positive correlations between relative sea-level rise and mangrove sediment accretion (Cahoon and Hensel, 2006), which contributes to mangroves keeping pace with regional relative sea-level rise. The rate of inorganic sediment accretion may decrease exponentially as the sediment elevation increases due to decreased tidal inundation frequency and duration (Allen, 1990, 1992; French, 1991, 1993; Saad et al., 1999; Woodroffe, 2002; Cahoon and Hensel, 2006). It is unclear how strong the feedback mechanism is, which is likely site-specific depending on the geomorphic setting and resulting sedimentation processes. Observations over decades and longer and from numerous sites from a range of settings experiencing rise, lowering and stability in relative sea-level, may improve the understanding of this and other feedback mechanisms. If sediment accretion does increase with increased hydroperiod (duration, frequency and depth of inundation), because increased sedimentation can increase mangrove plant growth through direct effects on elevation as well as increased nutrient delivery, this might further increase sediment accretion through organic matter deposition as well as enhanced sediment retention with the reduced rate of flow of floodwaters that would occur with higher tree productivity and root accumulation (Cahoon et al., 1999; McKee et al., 2007). This would be a negative feedback loop, as the increased sedimentation, and concomitant rise in elevation of the mangrove sediment surface, resulting from increased hydroperiod, would decrease the hydroperiod. Furthermore, increased hydroperiod may increase the mangrove substrate pore water storage (Cahoon et al., 1999), contributing to a rise in elevation of the sediment surface, reducing the hydroperiod.

The understanding of mangroves as opportunistic colonizers with distribution controlled through ecological responses to environmental factors (Tomlinson, 1986; Naidoo, 1985, 1990; Duke, 1992; Wakushima et al., 1994a,b; Duke et al., 1998; Cannicci et al., 2008) highlights the importance of the geomorphic setting in determining where mangrove ecosystems establish, their structure and functional processes (Woodroffe, 2002). An understanding of a mangrove's geomorphic setting, including sedimentation processes (sediment supply and type), hydrology, and energy regime, is likewise important in understanding resistance and responses to changes in sea-level, as these affect both surface and subsurface controls on elevation of the mangrove sediment surface. However, there has been no significant correlation observed between trends in mangrove sediment elevation and relative sea-level, tidal range, or soil bulk density, nor have correlations been observed between geomorphic class and trends in mangrove sediment elevation (Cahoon and Hensel, 2006). Until predictive sediment elevation models are developed for mangrove ecosystems, site-specific monitoring is necessary to assess vulnerability and responses to projected changes in sea-level.

2.1.2. *Mangrove responses to changes in relative sea-level*

When changing sea-level is the predominant factor controlling mangrove position, there are three general mangrove responses to sea-level trends:

- Stable site-specific relative sea-level: when sea-level is not changing relative to the mangrove surface, mangrove position is generally stable;
- Site-specific relative sea-level falling: when sea-level is falling relative to the mangrove surface, mangrove margins migrate seaward and possibly laterally if these areas adjacent to the mangrove develop conditions suitable for mangrove establishment; and
- Site-specific relative sea-level rising: if sea-level is rising relative to the elevation of the mangrove sediment surface, the mangrove's seaward and landward margins retreat landward as the mangrove species maintain their preferred hydroperiod. The mangrove may also expand laterally into areas of higher elevation. Environmental conditions for recruitment and establishment of mangroves in new areas that become available with relative sea-level rise include suitable hydrology and sediment composition, competition with non-mangrove plant species and availability of waterborne seedlings (Krauss et al., 2008). The seaward mangrove margin migrates landward from mangrove tree dieback due to stresses caused by a rising sea-level such as erosion resulting in weakened root structures and falling of trees, increased salinity, and too high a duration, frequency, and depth of inundation (Naidoo, 1983; Ellison, 1993, 2000, 2006; Lewis, 2005). Mangroves migrate landward via seedling recruitment and vegetative reproduction as new habitat becomes available landward through erosion, inundation, and concomitant change in salinity (Semeniuk, 1994). Depending on the ability of individual mangrove species to colonize newly available habitat at a rate that keeps pace with the rate of relative sea-level rise (Field, 1995; Duke et al., 1998; Lovelock and Ellison, 2007; Di Nitto et al., in press), slope of adjacent land and presence of obstacles to landward migration of the landward mangrove boundary (e.g.,

seawalls, roads), some mangroves will gradually be reduced in area, may revert to a narrow fringe, survival of individual trees or experience local extirpation.

Numerous factors other than change in relative sea-level can affect mangrove margin position, as well as structure and health. To predict mangrove responses to relative sea-level rise, it is necessary to determine if the change in sea-level is the predominant control over mangrove position and health, or if other stressors are predominant controls. Observation of a significant positive correlation between a change in relative sea-level and change in position of mangrove margins has been used to support the inference that change in site-specific relative sea-level is the predominant influence in determining the mangrove margin positions (Saintilan and Wilton, 2001; Wilton, 2002; Gilman et al., 2007a).

When sea-level rising relative to the elevation of the mangrove sediment surface is the predominant factor controlling mangrove position, mangrove responses over decades will generally follow trends shown by paleoenvironmental reconstructions of mangroves to past sea-level fluctuations (Woodroffe et al., 1985; Ellison and Stoddart, 1991; Woodroffe, 1995; Shaw and Ceman, 1999; Ellison, 1993, 2000; Berdin et al., 2003; Dahdouh-Guebas and Koedam, 2008; Ellison, 2008). Mangrove resistance and resilience to relative sea-level rise over human time scales are a result of four main factors: (i) the rate of change in sea-level relative to the mangrove sediment surface determines mangrove vulnerability (Cahoon and Hensel, 2006; Cahoon et al., 2006; Gilman et al., 2007b). (ii) Mangrove species composition affects mangrove responses: because different mangrove vegetation zones have different rates of change in sediment elevation (Krauss et al., 2003; Rogers et al., 2005b; McKee et al., 2007), some zones are more resistant and resilient to rising sea-level. Also, because mangrove species have differences in time required to colonize new habitat that becomes available with relative sea-level rise, the species that colonize more quickly may outcompete slower colonizers and become more dominant (Lovelock and Ellison, 2007). (iii) The physiographic setting, including the slope of land upslope from the mangrove relative to that of the land the mangrove currently occupies, and presence of obstacles to landward migration, affects mangrove resistance (Gilman et al., 2007a). Finally, (iv) cumulative effects of all stressors influence mangrove resistance and resilience. Mangroves are not expected to respond in accordance with Bruun rule (a predictive model of beach erosion) assumptions because mangroves have different sediment budget processes than beaches, and because predictive models of coastal erosion produce inaccurate results for small-scale, site-specific estimates (Bruun, 1988; List et al., 1997; Komar, 1998; Pilkey and Cooper, 2004).

2.2. *Extreme high water events*

The frequency of extreme high water events of a given height relative to fixed benchmarks is projected to increase over coming decades as a result of the same atmospheric and oceanic factors that are causing global sea-level to rise, and possibly also as a result of other influences on extremes such as variations in regional climate, like phases of the El Nino Southern Oscillation and North Atlantic Oscillation, through change in storminess and resulting storm surges (Woodworth and Blackman, 2004; Church et al., 2001, 2004b). For example, an analysis of 99th percentiles of hourly sea-level at 141 globally distributed stations for recent decades showed that there has been an increase in extreme high sea-level worldwide since 1975 (Woodworth and Blackman, 2004). In many cases, the secular changes in extremes were found to be similar to those in mean sea-level.

Increased frequency and levels of extreme high water events could affect the position and health of coastal ecosystems and pose a hazard to coastal development and human safety. Increased levels and frequency of extreme high water events may affect the position and health of mangroves in some of the same ways that storms have been observed to effect mangroves, including through altered sediment elevation and sulfide soil toxicity, however, the state of knowledge of ecosystem effects from changes in extreme waters is poor.

2.3. *Storms*

During the 21st century the Intergovernmental Panel on Climate Change projects that there is likely to be an increase in tropical cyclone peak wind intensities and increase in tropical cyclone mean and peak precipitation intensities in some areas as a result of global climate change (Houghton et al., 2001; Solomon et al., 2007). Storm surge heights are also predicted to increase if the frequency of strong winds and low pressures increase. This may occur if storms become more frequent or severe as a result of climate change (Church et al., 2001; Houghton et al., 2001; Solomon et al., 2007).

The increased intensity and frequency of storms has the potential to increase damage to mangroves through defoliation and tree mortality. In addition to causing tree mortality, stress, and sulfide soil toxicity, storms can alter mangrove sediment elevation through soil erosion, soil deposition, peat collapse, and soil compression (Smith et al., 1994; Woodroffe and Grime, 1999; Baldwin et al., 2001; Sherman et al., 2001; Woodroffe, 2002; Cahoon et al., 2003, 2006; Cahoon and Hensel, 2006; Piou et al., 2006). Areas suffering mass tree mortality with little survival of saplings and trees might experience permanent ecosystem conversion, as recovery through seedling recruitment might not occur due to the change in sediment elevation and concomitant change in hydrology (Cahoon et al., 2003). Other natural hazards, such as tsunami, which will not be affected by climate change, can also cause severe damage to mangroves and other coastal ecosystems (e.g., the 26 December 2004 Indian Ocean tsunami [Danielsen et al., 2005; Kathiresan and Rajendran, 2005; Dahdouh-Guebas et al., 2005a,b, 2006]).

2.4. *Precipitation*

Globally, rainfall is predicted to increase by about 25% by 2050 in response to climate change. However, the regional distribution of rainfall will be uneven (Houghton et al., 2001).

Increased precipitation is very likely in high-latitudes, and decreased precipitation is likely in most subtropical regions, especially at the poleward margins of the subtropics (Solomon et al., 2007). In the most recent assessment, the Intergovernmental Panel on Climate Change reported significant increases in precipitation in eastern parts of North and South America, northern Europe and northern and central Asia, with drying in the Sahel, the Mediterranean, southern Africa and parts of southern Asia (Solomon et al., 2007). Long-term trends had not been observed for other regions.

Changes in precipitation patterns are expected to affect mangrove growth and spatial distribution (Field, 1995; Ellison, 2000). Based primarily on links observed between mangrove habitat condition and rainfall trends (Field, 1995; Duke et al., 1998), decreased rainfall and increased evaporation will increase salinity, decreasing net primary productivity, growth and seedling survival, altering competition between mangrove species, decreasing the diversity of mangrove zones, causing a notable reduction in mangrove area due to the conversion of upper tidal zones to hypersaline flats. Areas with decreased precipitation will have a smaller water input to groundwater and less freshwater surface water input to mangroves, increasing salinity. As soil salinity increases, mangrove trees will have increased tissue salt levels and concomitant decreased water availability, which reduces productivity (Field, 1995). Increased salinity will increase the availability of sulfate in seawater, which would increase anaerobic decomposition of peat, increasing the mangrove's vulnerability to any rise in relative sea-level (Snedaker, 1993, 1995). Reduced precipitation can result in mangrove encroachment into salt marsh and freshwater wetlands (Saintilan and Wilton, 2001; Rogers et al., 2005a).

Increased rainfall will result in increased growth rates and biodiversity, increased diversity of mangrove zones, and an increase in mangrove area, with the colonization of previously unvegetated areas of the landward fringe within the tidal wetland zone (Field, 1995; Duke et al., 1998). For instance, mangroves tend to be taller and more diverse on high rainfall shorelines relative to low rainfall shorelines, as observed in most global locations, including Australia (Duke et al., 1998). Areas with higher rainfall have higher mangrove diversity and productivity probably due to higher supply of fluvial sediment and nutrients, as well as reduced exposure to sulfate and reduced salinity (McKee, 1993; Field, 1995; Ellison, 2000). Mangroves will likely increase peat production with increased freshwater inputs and concomitant reduced salinity due to decreased sulfate exposure (Snedaker, 1993, 1995).

These predicted responses are based on assessments from only a few areas and are currently untested in longitudinal studies at any single location. Further research is needed to confirm these hypotheses and to assess the broader significance of rainfall variability on mangroves.

2.5. Temperature

Between 1906 and 2005, the global average surface temperature has increased by 0.74 °C (±0.18 °C) (Solomon et al., 2007). The linear warming trend of the last fifty years (0.13 °C per decade) is nearly twice that for the last 100 years. This rise in globally averaged temperatures since the mid-20th century is considered to be very likely due to the observed increase in anthropogenic greenhouse gas atmospheric concentrations (Solomon et al., 2007). The range in projections for the rise in global averaged surface temperatures from 1980 to 1999 to the end of the 21st century (2090–2099) is 1.1–6.4 °C (Solomon et al., 2007).

Increased surface temperature is expected to affect mangroves by (Field, 1995; Ellison, 2000):

(i) changing species composition;
(ii) changing phenological patterns (e.g., timing of flowering and fruiting);
(iii) increasing mangrove productivity where temperature does not exceed an upper threshold; and
(iv) expanding mangrove ranges to higher latitudes where range is limited by temperature, but is not limited by other factors, including a supply of propagules and suitable physiographic conditions.

Mangroves reach a latitudinal limit at the 16 °C isotherm for air temperature of the coldest month, and the margins of incidence of ground frost, where water temperatures do not exceed 24 °C (Ellison, 2000). The optimum mangrove leaf temperature for photosynthesis is believed to be between 28 and 32 °C, while photosynthesis ceases when leaf temperatures reach 38–40 °C (Clough et al., 1982; Andrews et al., 1984).

The frequency, duration and intensity of extreme cold events have been hypothesized to explain the current latitudinal limits of mangrove distribution (Woodroffe and Grindrod, 1991; Snedaker, 1995). However, the incidence of extreme cold events is not likely to be a factor limiting mangrove expansion to higher latitudes in response to increased surface temperature. The Intergovernmental Panel on Climate Change projects reduced extreme cold events (Solomon et al., 2007), in correlation with projected changes in average surface temperatures. For instance, Vavrus et al. (2006) predicted a 50–100% decline in the frequency of extreme cold air events in Northern Hemisphere winter in most areas, while Meehl et al. (2004) projected decreases in frost days in the extratropics, where the pattern of decreases will be determined by changes in atmospheric circulation.

2.6. Atmospheric CO_2 concentration

The atmospheric concentration of CO_2 has increased 35% from a pre-industrial value, from 280 parts per million by volume (ppmv) in 1880 to 379 ppmv in 2005 (Solomon et al., 2007). In recent decades, CO_2 emissions have continued to increase: CO_2 emissions increased from an average of 6.4 ± 0.4 GtC a^{-1} in the 1990s to 7.2 ± 0.3 GtC a^{-1} in the period 2000–2005.

A direct effect of elevated atmospheric CO_2 levels may be increased productivity of some mangrove species (Field, 1995; Ball et al., 1997; Komiyama et al., 2008). Mangrove metabolic responses to increased atmospheric CO_2 levels are likely to be increased growth rates (Farnsworth et al., 1996) and more efficient regulation of water loss (UNEP, 1994). For some mangrove species, the response to elevated CO_2 may be sufficient to induce substantial change of vegetation along natural salinity and aridity gradients. Ball et al. (1997) showed that doubled CO_2 had little effect on mangrove growth rates in hypersaline areas, and this may combine with reduced rainfall to create some stress. The greatest effect may be under low salinity conditions. Elevated CO_2 conditions may enhance the growth of mangroves when carbon gain is limited by evaporative demand at the leaves but not when it is limited by salinity at the roots. There is no evidence that elevated CO_2 will increase the range of salinities in which mangrove species can grow. The conclusion is that whatever growth enhancement may occur at salinities near the limits of tolerance of a species, it is unlikely to have a significant effect on ecological patterns (Ball et al., 1997). However, not all species may respond similarly, and other environmental factors, including temperature, salinity, nutrient levels and the hydrologic regime, may influence how a mangrove wetland responds to increased atmospheric CO_2 levels (Field, 1995). The effect of enhanced CO_2 on mangroves is poorly understood and there is a paucity of research in this area.

Table 2
Adaptation options to augment mangrove resistance and resilience to climate change

Adaptation option	Description
"No regrets" reduction of stresses	Eliminate non-climate stresses on mangroves (e.g., filling, conversion for aquaculture, pollution) in order to augment overall ecosystem health, in part, to reduce mangrove vulnerability to and increase resilience to stresses from climate change. These "no regrets" mitigation actions are justified and beneficial even in the absence of adverse effects on mangroves from climate change (Adger et al., 2007; Julius and West, 2007).
Manage activities in catchment that affect mangrove sediment elevation	In order to attempt to augment mangrove resistance to sea-level rise relative to the mangrove sediment surface, activities within the mangrove catchment can be managed to minimize long-term reductions in mangrove sediment elevation, or enhance sediment elevation. For instance, limiting development of impervious surfaces within the mangrove catchment and managing rates and locations of groundwater extraction can reduce alteration to natural groundwater recharge to the mangrove systems, which might be an important control on mangrove elevation. Also, avoiding and limiting human activities that reduce mangrove soil organic matter accumulation, such as the diversion of sediment inputs to mangrove systems, nutrient and pollutant inputs into mangroves, and mangrove timber harvesting can contribute to maintaining relatively natural controls on trends in sediment elevation. Depending on the tree species and nutrient added, nutrient enrichment can affect mangrove productivity, changing root production and organic material inputs, changing the rate of change in sediment elevation (Feller et al., 2003; McKee et al., 2002, 2007). Enhancement of mangrove sediment accretion rates, such as through the beneficial use of dredge spoils, could augment mangrove sediment elevation (Lewis, 1990), but would need to avoid excessive or sudden sediment deposition (Ellison, 1998).
Managed retreat	Site planning for some sections of shoreline containing mangroves, such as areas that are not highly developed, may facilitate long-term retreat with relative sea-level rise (Dixon and Sherman, 1990; Mullane and Suzuki, 1997; Gilman, 2002). "Managed retreat" involves implementing land-use planning mechanisms before the effects of rising sea-level become apparent, which can be planned carefully with sufficient lead time to enable economically viable, socially acceptable and environmentally sound management measures. Coastal development could remain in use until the eroding coastline becomes a safety hazard or begins to prevent landward migration of mangroves, at which time the development can be abandoned or moved inland. Adoption of legal tools, such as rolling easements, can help make eventual abandonment more acceptable (Titus, 1991). Zoning rules for building setbacks and permissible types of new development can be used to reserve zones behind current mangroves for future mangrove habitat. Managers can determine adequate setbacks by assessing site-specific rates for landward migration of the mangrove landward margin. Construction codes can plan for mangrove landward migration based on a desired lifetime for coastal development (Mullane and Suzuki, 1997). Any new construction of minor coastal development structures, such as sidewalks and boardwalks, could be required to be expendable with a lifetime based on the assessed sites' erosion rate and selected setback. Rules could prohibit construction of coastal engineering structures, which obstruct natural inland migration of mangroves. This managed coastal retreat will allow mangroves to migrate and retain their natural functional processes.
Fortification	While mangroves provide natural coastal protection that is expensive to replace with artificial structures (Mimura and Nunn, 1998; Walters et al., 2008), for some sections of highly developed coastline adjacent to mangroves, site planning may justify use of hard engineering technology (e.g., groins, seawalls, revetments, bulkheads) and other shoreline erosion control measures (e.g., surge breakers, dune fencing, detached breakwaters) to halt erosion. As a result, mangrove ecosystem services will gradually be reduced: The structure will prevent the mangroves' natural landward migration and the mangrove fronting the structure, as well as immediately downstream in the direction of longshore sediment transport from the structure, will eventually be converted to deepwater habitat (Tait and Griggs, 1990; Fletcher et al., 1997; Mullane and Suzuki, 1997; Mimura and Nunn, 1998).

Table 2 (*Continued*)

Adaptation option	Description
Representation, replication and refugia through a system of protected area networks	Protected areas can be established and managed to implement mangrove representation, replication and refugia. Ensuring representation of all mangrove community types when establishing a network of protected areas and replication of identical communities to spread risk can increase chances for mangrove ecosystems surviving climate change and other stresses (Julius and West, 2007). Ensuring that a portfolio of each different community type is represented is a strategy for optimizing climate change resilience as this representation increases the change that at least one of these communities with disparate physical and biological parameters will survive climate change stressors and provide a source for re-colonizing. Replication, through the protection of multiple areas of each mangrove community type, by protecting multiple examples of each vegetation zone and geomorphic setting can help avoid the loss of a single community type (Roberts et al., 2003; Salm et al., 2006; Wells, 2006). Protected area selection can include mangrove areas that act as climate change refugia, communities that are likely to be more resistant to climate change stresses (Palumbi et al., 1997; Bellwood and Hughes, 2001; Salm et al., 2006). For instance, mature mangrove communities will be more resistant and resilient to stresses, including those from climate change, than recently established forests. Protecting refugia areas that resist and/or recover quickly from disturbance in general, or that are predicted to be able to keep pace with projected relative sea-level rise can serve as a source of recruits to re-colonize areas that are lost or damaged. Protected area site selection should account for predicted ecosystem responses to climate change (Barber et al., 2004). For instance, planners need to account for the likely movements of habitat boundaries and species ranges over time under different sea-level and climate change scenarios, as well as consider an areas' resistance and resilience to projected sea-level and climate changes and contributions to adaptation strategies. Site-specific analysis of resistance and resilience to climate change when selecting areas to include in new protected areas should include, for example, how discrete coastal habitats might be blocked from natural landward migration, and how severe are threats not related to climate change in affecting the site's health. A system of networks of protected areas can be designed to protect connectivity between coastal ecosystems, including mangroves (Crowder et al., 2000; Stewart et al., 2003; Roberts et al., 2001, 2003). Protecting a series of mature, healthy mangrove sites along a coastline could increase the likelihood of there being a source of waterborne seedlings to re-colonize sites that are degraded. Protected area designs should include all coastal ecosystems to maintain functional links (Mumby et al., 2004).
Mangrove rehabilitation	Mangrove enhancement (removing stresses that caused their decline) can augment resistance and resilience to climate change, while mangrove restoration (ecological restoration, restoring areas where mangrove habitat previously existed) (Kusler and Kentula, 1990; Lewis, 2005; Lewis et al., 2006; Bosire et al., 2008) can offset anticipated losses from climate change.
Regional monitoring network	Given uncertainties about future climate change and responses of mangroves and other coastal ecosystems, there is a need to monitor and study changes systematically. Establishing mangrove baselines and monitoring gradual changes through regional networks using standardized techniques will enable the separation of site-based influences from global changes to provide a better understanding of mangrove responses to sea-level and global climate change, and alternatives for mitigating adverse effects (CARICOMP, 1998; Ellison, 2000). For instance, coordinated observations of regional phenomena such as a mass mortality event of mangrove trees, or trend in reduced recruitment levels of mangrove seedlings, might be linked to observations of changes in regional climate such as reduced precipitation. The monitoring system, while designed to distinguish climate change effects on mangroves, would also therefore show local effects, providing coastal managers with information to abate these sources of degradation (a ''no-regrets'' adaptation approach).
Outreach and education	Outreach and education activities can augment community support for adaptation actions. The value of wetlands conservation is often underestimated, especially in less developed countries with high population growth and substantial development pressure, where short-term economic gains that result from activities that adversely affect wetlands are often preferred over the less-tangible long-term benefits that accrue from sustainably using wetlands. Education and outreach programs are an investment to bring about changes in behavior and attitudes by having a better informed community of the value of mangroves and other ecosystems. This increase in public knowledge of the importance of mangroves provides the local community with information to make informed decisions about the use of their mangrove resources, and results in grassroots support and increased political will for measures to conserve and sustainably manage mangroves.

2.7. *Ocean circulation patterns*

Key oceanic water masses are changing, however, the Intergovernmental Panel on Climate Change reports that at present, there is no clear evidence for ocean circulation change (Bindoff et al., 2007). However, there have been observations of long-term trends in changes in global and basin-scale ocean heat content and salinity, which are linked to changes in ocean circulation (Gregory et al., 2005; Bindoff et al., 2007).

Changes to ocean surface circulation patterns may affect mangrove propagule dispersal and the genetic structure of mangrove populations, with concomitant effects on mangrove community structure (Duke et al., 1998; Benzie, 1999; Lovelock and Ellison, 2007). Increasing gene flow between currently separated populations and increasing mangrove species diversity could increase mangrove resistance and resilience.

2.8. Adjacent ecosystem responses

Coral reefs, seagrass beds, estuaries, beaches, and coastal upland ecosystems may experience reduced area and health from climate change outcomes, including increased temperature, timing of seasonal temperature changes, and ocean acidification (Harvell et al., 2002; Kleypas et al., 2006; Mydlarz et al., 2006). Mangroves are functionally linked to neighboring coastal ecosystems, including seagrass beds, coral reefs, and upland habitat, although the functional links are not fully understood (Mumby et al., 2004). Degradation of adjacent coastal ecosystems from climate change and other sources of stress may reduce mangrove health. For instance, mangroves of low islands and atolls, which receive a proportion of sediment supply from productive coral reefs, may suffer lower sedimentation rates and increased susceptibility to relative sea-level rise if coral reefs become less productive due to relative sea-level rise or other climate change outcomes.

2.9. Human responses

Anthropogenic responses to climate change have the potential to exacerbate the adverse effects of climate change on mangrove ecosystems. For instance, we can expect an increase in the construction of seawalls and other coastal erosion control structures adjacent to mangrove landward margins as the threat to development from rising sea-levels and concomitant coastal erosion becomes increasingly apparent. Seawalls and other erosion control structures cause erosion and scouring of the mangrove immediately fronting and down-current from the structure (Table 2) (Tait and Griggs, 1990; Fletcher et al., 1997; Mullane and Suzuki, 1997). Or, for example, areas experiencing reduced precipitation and rising temperature may have increased groundwater extraction to meet the demand for drinking water and irrigation. Increased groundwater extraction will increase sea-level rise rates relative to mangrove surfaces (Krauss et al., 2003), increasing mangrove vulnerability. Increased rainfall could lead to increased construction of stormwater drainage canals to reduce flooding of coastal upland areas, diverting surface water from mangroves and other coastal systems, reducing mangrove productivity.

3. Adaptation options

To reduce the risk of adverse outcomes from predicted mangrove responses to projected climate change, adaptation activities can be taken in an attempt to increase the resistance and resilience of ecosystems to climate change stressors (Scheffer et al., 2001; Turner et al., 2003; Tompkins and Adger, 2004; Julius and West, 2007). Alternative options for adaptation for climate-sensitive ecosystems, including mangroves, are summarized in Table 2.

Mangrove ecosystems were able to persist through the quaternary despite substantial disruptions from large sea-level fluctuations, demonstrating that mangroves are highly resilient to change over historic time scales (Woodroffe, 1987, 1992). However, over coming decades, mangrove vulnerability and responses to climate change will be highly influenced by anthropogenic disturbances, including direct sources of degradation such as clearing and filling, and human responses to climate change that adversely affect mangroves. Measures can be taken to avoid and minimize these anthropogenic sources of stress (Table 2), which reduce mangrove resistance and resilience to climate change.

Management authorities are encouraged to assess coastal ecosystem vulnerability to climate change and institute appropriate adaptation measures to provide adequate lead time to avoid and minimize social disruption and cost, minimize losses of coastal ecosystem services, and maximize available options. The selection of adaptation strategies is likely to be made as part a broader coastal site-planning process, where mitigation actions are typically undertaken to address both climate and non-climate threats (Gilman, 2002; Adger et al., 2007). This analysis requires balancing multiple and often conflicting objectives of allowing managers and stakeholders to sustain the provision of ecological, economic, and cultural values; address priority threats to natural ecosystem functioning; maintain ecological processes and biodiversity; achieve sustainable development; and fulfill institutional, policy, and legal needs (Gilman, 2002).

4. Conclusions

To date, relative sea-level rise has likely been a smaller threat to mangroves than non-climate related anthropogenic stressors, which have likely accounted for most of the global average annual rate of mangrove loss, estimated to be 1–2%, with losses during the last quarter century ranging between 35 and 86% (Valiela et al., 2001; FAO, 2003; Duke et al., 2007). However, relative sea-level rise may constitute a substantial proportion of predicted future losses: Studies of mangrove vulnerability to change in relative sea-level, primarily from the western Pacific and Wider Caribbean regions, have documented that the majority of mangrove sites have not been keeping pace with current rates of relative sea-level rise (Cahoon et al., 2006; Cahoon and Hensel, 2006; Gilman et al., 2007b; McKee et al., 2007). Longer term studies are needed to determine if these are long-term trends or cyclical short-term patterns, and whether this is a global or regional phenomenon. Extrapolating from results in American Samoa on mangrove resilience to relative sea-level rise, a 0.2% average annual reduction in mangrove area for the Pacific Islands region is predicted over the next century based on relative sea-level trends and physiographic settings (Gilman et al., 2006). Based on this limited information, relative sea-level rise could be a substantial cause of future reductions in regional mangrove area, contributing about 10–20% of total estimated losses.

Mangrove forests occupy an inter-tidal habitat, and are extensively developed on accretionary shorelines, where sediment supply, in combination with subsurface processes that affect sediment elevation, determines their ability to keep up with sea-level rise. Rising sea-level will have the greatest impact on mangroves experiencing net lowering in sediment elevation, that are in a physiographic setting that provides limited area for landward migration due to obstacles or steep gradients.

Direct climate change impacts on mangrove ecosystems are likely to be less significant than the effects of associated sea-level rise. Rise in temperature and the direct effects of increased CO_2 levels are likely to increase mangrove productivity, change the timing of flowering and fruiting, and expand the ranges of mangrove species into higher latitudes. Changes in precipitation and subsequent changes in aridity may affect the distribution of mangroves. However, outcomes of global climate change besides sea-level rise are less certain, and the responses of mangrove ecosystems to changes in these parameters are not well understood. The understanding of the synergistic effects of multiple climate change and other anthropogenic and natural stressors on mangroves is also poor. For example, a mangrove that is experiencing an elevation deficit to rising sea-level may be located in an area experiencing decreased precipitation, where groundwater extraction for drinking water is predicted to increase. The combined effect of just these three stresses on the mangrove could result in an accelerated rate of rise in sea-level relative to the mangrove sediment surface, and at the same time decreased productivity, resulting in highly compromised resistance and resilience to stresses from climate change and other sources. Models have not been developed to predict the effects of multiple stresses such as described in this hypothetical example. There is an urgent need to test the hypotheses that have been advanced on the likely effects of global climate change on mangroves as there are many uncertainties and the effects are likely to be felt over a very long time scale.

Reduced mangrove area and health and landward mangrove migration will increase the threat to human safety and shoreline development from coastal hazards such as erosion, flooding, and storm waves and surges. Predicted mangrove losses will also reduce coastal water quality, reduce biodiversity, eliminate fish nursery habitat, adversely affect adjacent coastal habitats (Mumby et al., 2004), and eliminate a major resource for human communities that traditionally rely on mangroves for numerous products and services (Ewel et al., 1998; Walters et al., 2008). There is a need to better plan our responses to climate change impacts on mangroves, especially in its identification through regional monitoring networks, and coastal planning that facilitates mangrove migration with sea-level rise and incorporates understanding of the consequence of shoreline changes. The resistance and resilience of mangroves to sea-level rise and other climate change impacts can be improved by better "no regrets" management of other stressors on mangrove area and health, strategic planning of protected areas including mangroves and functionally linked ecosystems, rehabilitation of degraded mangroves, and outreach and education directed at communities residing adjacent to mangroves.

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References

Adger, W.N., Agrawala, S., Mirza, M.M.Q., Conde, C., O'Brien, K., Pulhin, J., Pulwarty, R., Smit, B., Takahashi, K., 2007. Assessment of adaptation practices, options, constraints and capacity. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 717–743.

Allen, J.R., 2000. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. Quat. Sci. Rev. 19, 1155–1231.

Allen, J.R., 1992. Tidally induced marshes in the Severn Estuary, southwest Britain. In: Allen, J.R., Pye, K. (Eds.), Saltmarshes: Morphodynamics, Conservation and Engineering Significance. Cambridge University Press, Cambridge, pp. 123–147.

Allen, J.R., 1990. Constraints on measurement of sea level movements from salt-marsh accretion rates. J. Geol. Soc. Lond. 147, 5–7.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Andrews, T.J., Clough, B.F., Muller, G.J., 1984. Photosynthetic gas exchange properties and carbon isotope ratios of some mangroves in North Queensland. In: Teas, H.J. (Ed.), Physiology and Management of Mangroves, Tasks for Vegetation Science, vol. 9. Dr. W. Junk, The Hague, pp. 15–23.

Baldwin, A., Egnotovich, M., Ford, M., Platt, W., 2001. Regeneration in fringe mangrove forests damaged by Hurricane Andrew. Plant Ecol. 157, 149–162.

Ball, M.C., Cochrane, M.J., Rawason, H.M., 1997. Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentration of atmospheric CO_2. Plant Cell Environ. 20, 1158–1166.

Barber, C.V., Miller, K., Boness, M. (Eds.), 2004. Securing Protected Areas in the Face of Global Change: Issues and Strategies. IUCN, Gland, Switzerland.

Bellwood, D.R., Hughes, T., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science 292, 1532–1534.

Bennett, E.M., Cumming, G.S., Peterson, G.D., 2005. A systems model approach to determining resilience surrogates for case studies. Ecosystems 8, 945–957.

Benzie, J.A.H., 1999. Genetic structure of coral reef organisms, ghosts of dispersal past. Am. Zool. 39, 131–145.

Berdin, R., Siringan, F., Maeda, Y., 2003. Holocene relative sea-level changes and mangrove response in Southwest Bohol, Philippines. J. Coast. Res. 19, 304–313.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of Individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Bindoff, N.L., Willebrand, J., Artale, V., Cazenave, A., Gregory, J., Gulev, S., Hanawa, K., Le Quéré, C., Levitus, S., Nojiri, Y., Shum, C., Talley, L., Unnikrishnan, A., 2007. Observations: oceanic climate change and sea level. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., Tignor, M., Miller, H. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Boumans, R.M.J., Day Jr., J.W., 1993. High precision measurements of sediment elevation in shallow coastal areas using a sediment-erosion table. Estuaries 16, 375–380.

Bruun, P., 1988. The Bruun Rule of Erosion by sea-level rise: a discussion of large-scale two and three-dimensional usages. J. Coast. Res. 4, 627–648.

Cahoon, D.R., Hensel, P., 2006. High-resolution global assessment of mangrove responses to sea-level rise: a review. In: Gilman, E. (Ed.), Proceedings of the Symposium on Mangrove Responses to Relative Sea Level Rise and Other Climate Change Effects, 13 July 2006, Catchments to Coast, Society of Wetland Scientists 27th International Conference, 9–14 July 2006, Cairns Convention Centre, Cairns, Australia. Western Pacific Regional Fishery Management Council, Honolulu, HI, USA, ISBN: 1-934061-03-4 pp. 9–17.

Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L., Saintilan, N., 2006. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In: Verhoeven, J.T.A., Beltman, B., Bobbink, R., Whigham, D. (Eds.), Wetlands and Natural Resource Management. Ecological Studies, vol. 190. Springer-Verlag, Berlin/Heidelberg, pp. 271–292.

Cahoon, D.R., Hensel, P., Rybczyk, J., McKee, K., Proffitt, C.E., Perez, B., 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. J. Ecol. 91, 1093–1105.

Cahoon, D.R., Lynch, J.C., Hensel, P., Boumans, R., Perez, B.C., Segura, B., Day Jr., J.W., 2002. A device for high precision measurement of wetland sediment elevation: I. Recent improvements to the sedimentation-erosion table. J. Sediment. Res. 72, 730–733.

Cahoon, D.R., Day, J.W., Reed, D.J., 1999. The influence of surface and shallow subsurface soil processes on wetland elevation, a synthesis. Curr. Topics Wetland Biogeochem. 3, 72–88.

Cahoon, D.R., Lynch, J.C., 1997. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, USA. Mangroves Salt Marshes 1, 173–186.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

CARICOMP, 1998. Caribbean Coastal Marine Productivity (CARICOMP): a Cooperative Research and Monitoring Network of Marine Laboratories, Parks, and Reserves. CARICOMP Methods Manual Level 1. Manual of Methods for Mapping and Monitoring of Physical and Biological Parameters in the Coastal Zone of the Caribbean. CARICOMP Data Management Center, Centre for Marine Sciences, University of the West Indies, Mona, Kingston, Jamaica.

Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4, 765–781.

Cazenave, A., Nerem, R., 2004. Present-day sea level change: observations and causes. Rev. Geophys. 42, 1–20.

Church, J., White, N., 2006. A 20th century acceleration in global sea-level rise. Geophys. Res. Lett. 33, L01602.

Church, J., White, N., Coleman, R., Lambeck, K., Mitrovica, J., 2004a. Estimates of the regional distribution of sea-level rise over the 1950 to 2000 period. J. Climate 17, 2609–2625.

Church, J., Hunter, J., McInnes, K., White, N., 2004b. Sea-level rise and the frequency of extreme events around the Australian coastline. In: Coast to Coast '04—Conference Proceedings Australia's National Coastal Conference, Hobart, 19–23 April 2004, pp. 1–8.

Church, J., Gregory, J., Huybrechts, P., Kuhn, M., Lambeck, K., Nhuan, M., Qin, D., Woodworth, P., 2001. Changes in sea level. In: Houghton, J., Ding, Y., Griggs, D., Noguer, M., van der Linden, P., Dai, X., Maskell, K., Johnson, C. (Eds.), Climate Change 2001: The Scientific Basis (Published for the Intergovernmental Panel on Climate Change). Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA, (Chapter 11), pp. 639–693.

Clough, B.F., Andrews, T.J., Cowan, I.R., 1982. Physiological processes in mangroves. In: Clough, B.F. (Ed.), Mangrove Ecosystems in Australia: Structure, Function and Management. Australian National University Press, Canberra, pp. 193–210.

Crowder, L.B., Lyman, S., Figueira, W., Priddy, J., 2000. Source-sink population dynamics and the problem of siting marine reserves. Bull. Mar. Sci. 66, 799–820.

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., LoSeen, D., Koedam, N., 2005a. How effective were mangroves as a defence against the recent tsunami? Curr. Biol. 15, R443–R447.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005b. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Koedam, N., Danielsen, F., Sørensen, M.K., Olwig, M.F., Selvam, V., Parish, F., Burgess, N.D., Topp-Jørgensen, E., Hiraishi, T., Karunagaran, V.M., Rasmussen, M.S., Hansen, L.B., Quarto, A., Suryadiputra, N., 2006. Coastal vegetation and the Asian tsunami. Science 311, 37–38.

Danielsen, F., Soerensen, M., Olwig, M., Selvam, V., Parish, F., Burgess, N., Hiraishi, T., Karunagaran, V., Rasmussen, M., Hansen, L., Quarto, A., Nyoman, S., 2005. The Asian tsunami: a protective role for coastal vegetation. Science 310, 643.

Dahdouh-Guebas, F., Koedam, N., 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: A review. Aquat. Bot. 89, 80–92.

Di Nitto, D., Dahdouh-Guebas, F., Kairo, J.G., Decleir H., Koedam, N. Sea level rise effects on mangrove propagule establishment: experimental study using digital terrain modeling. Mar. Ecol. Prog. Ser., in press.

Dixon, J.A., Sherman, P.B., 1990. Economics of Protected Areas. A New Look at Benefits and Costs. Island Press, Washington, DC, USA.

Duke, N.C., Meynecke, J.O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecol. Biogeogr. 7, 27–47.

Duke, N.C., 1992. Mangrove floristics and biogeography. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, USA, pp. 63–100.

Ellison, J.C., 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: A review. Aquat. Bot. 89, 93–104.

Ellison, J., 2006. Mangrove paleoenvironmental response to climate change. In: Gilman, E. (Ed.), Proceedings of the Symposium on Mangrove Responses to Relative Sea-Level Rise and Other Climate Change Effects, Society of Wetland Scientists 2006 Conference, 9–14 July 2006, Cairns, Australia. Western Pacific Regional Fishery Management Council and United Nations Environment Programme Regional Seas Programme, Honolulu, USA and Nairobi, Kenya, ISBN: 1-934061-03-4 pp. 1–8.

Ellison, J., 2000. How South Pacific mangroves may respond to predicted climate change and sea level rise. In: Gillespie, A., Burns, W. (Eds.), Climate Change in the South Pacific: Impacts and Responses in Australia, New Zealand, and Small Islands States. Kluwer Academic Publishers, Dordrecht, Netherlands, (Chapter 15), pp. 289–301.

Ellison, J.C., 1998. Impacts of sediment burial on mangroves. Mar. Pollut. Bull. 37, 8–12.

Ellison, J., 1993. Mangrove retreat with rising sea level, Bermuda. Estuar. Coast. Shelf Sci. 37, 75–87.

Ellison, J., Stoddart, D., 1991. Mangrove ecosystem collapse during predicted sea level rise: Holocene analogues and implications. J. Coast. Res. 7, 151–165.

Ewel, K.C., Twilley, R.R., Ong, J.E., 1998. Different kinds of mangrove forests provide different goods and services. Global Ecol. Biogeogr. 7, 83–94.

FAO, 2003. Status and Trends in Mangrove Area Extent Worldwide. Food and Agriculture Organization of the United Nations, Forest Resources Division, Paris.

Farnsworth, E.J., Ellison, A.M., Gong, W.K., 1996. Elevated CO_2 alters anatomy, physiology, growth and reproduction of red mangrove (*Rhizophora mangle* L.). Oecologia 108, 599–609.

Feller, I.C., McKee, K.L., Whigham, D.F., O'Neill, J.P., 2003. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62, 145–175.

Field, C., 1995. Impacts of expected climate change on mangroves. Hydrobiologia 295, 75–81.

Fletcher, C.H., Mullane, R.A., Richmond, B., 1997. Beach loss along armored shorelines of Oahu, Hawaiian Islands. J. Coast. Res. 13, 209–215.

French, J.R., 1993. Numerical simulation of vertical marsh growth and adjustment to accelerated sea-level rise, North Norfolk, UK. Earth Surf. Proc. Land 18, 63–81.

French, J.R., 1991. Eustatic and neotectonic controls on salt marsh sedimentation. In: Kraus, N.C., Gingerich, K.J., Kriebel, D.L. (Eds.), Coastal Sediments '91. American Society of Civil Engineers, New York, pp. 1223–1236.

Furukawa, K., Wolanski, E., Mueller, H., 1997. Currents and sediment transport in mangrove forests. Estuar. Coast. Shelf Sci. 44, 301–310.

Furukawa, K., Wolanski, E., 1996. Sedimentation in mangrove forests. Mangroves Salt Marshes 1, 3–10.

Gilman, E., Ellison, J., Coleman, R., 2007a. Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. Environ. Monit. Assess. 124, 112–134.

Gilman, E., Ellison, J., Sauni Jr., I., Tuaumu, S., 2007b. Trends in surface elevations of American Samoa mangroves. Wetl. Ecol. Manag. 15, 391–404.

Gilman, E., Ellison, J., Jungblat, V., VanLavieren, H., Wilson, L., Areki, F., Brighouse, G., Bungitak, J., Dus, E., Henry, M., Sauni Jr., I., Kilman, M., Matthews, E., Teariki-Ruatu, N., Tukia, S., Yuknavage, K., 2006. Adapting to Pacific Island mangrove responses to sea level rise and other climate change effects. Climate Res. 32, 161–176.

Gilman, E.L., 2002. Guidelines for coastal and marine site-planning and examples of planning and management intervention tools. Ocean Coast. Manag. 45, 377–404.

Gregory, J.M., Dixon, K.W., Stouffer, R.J., Weaver, A.J., Driesschaert, E., Eby, M., 2005. A model intercomparison of changes in the Atlantic thermohaline circulation in response to increasing atmospheric CO_2 concentration. Geophys. Res. Lett. 32, L12703.

Hansen, L.J., Biringer, J., 2003. Building resistance and resilience to climate change. In: Hansen, L.J., Biringer, J.L., Hoffmann, J.R. (Eds.), Buying Time: A User's Manual for Building Resistance and Resilience to Climate Change in Natural Systems. WWF Climate Change Program, Berlin, Germany, pp. 9–14.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296, 2158–2162.

Holgate, S.J., Woodworth, P.L., 2004. Evidence for enhanced coastal sea level rise during the 1990s. Geophys. Res. Lett. 31, L07305.

Houghton, J., Ding, Y., Griggs, D., Noguer, M., van der Linden, P., Dai, X., Maskell, K., Johnson, C. (Eds.), 2001. Climate Change 2001: The Scientific Basis (Published for the Intergovernmental Panel on Climate Change). Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA.

IUCN, 1989. The impact of climatic change and sea level rise on ecosystems. Report for the Commonwealth Secretariat, London.

Julius, S.H., West, J.M. (Eds.), 2007. Draft. Preliminary Review of Adaptation Options for Climate-Sensitive Ecosystems and Resources. Synthesis and Assessment Product 4.4. U.S. Climate Change Science Program. U.S. Environmental Protection Agency, Washington, DC, USA.

Kathiresan, K., Rajendran, N., 2005. Coastal mangrove forests mitigated tsunami. Estuar. Coast. Shelf Sci. 65, 601–606.

Kleypas, J.A., Feely, R.A., Fabry, V.J., Langdon, C., Sabine, C.L., Robbins, L.L., 2006. Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Workshop Report. National Science Foundation, National Oceanic and Atmospheric Administration, and the U.S. Geological Survey, Washington, DC

Komar, P., 1998. Beach Processes and Sedimentation, second ed. Prentice Hall, Upper Saddle River, NJ, USA.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Krauss, K.W., Allen, J.A., Cahoon, D.R., 2003. Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests. Estuar. Coast. Shelf Sci. 56, 251–259.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Kusler, J.A., Kentula, M.E. (Eds.), 1990. Wetland Creation and Restoration: The Status of the Science. Island Press, Washington, DC, USA.

Lewis III, R.R., Erftemeijer, P., Hodgson, A., 2006. A novel approach to growing mangroves on the coastal mud flats of Eritrea with the potential for relieving regional poverty and hunger: comment. Wetlands 26, 637–638.

Lewis III, R.R., 2005. Ecological engineering for successful management and restoration of mangrove forests. Ecol. Eng. 24, 403–418.

Lewis III, R.R., 1992. Scientific perspectives on on-site/off-site, in-kind/out-of-kind mitigation. In: Kusler, J.A., Lassonde, C. (Eds.), Effective Mitigation: Mitigation Banks and Joint Projects in the Context of Wetland Management Plans. Proceedings of the National Wetland Symposium, 24–27 June 1992, Palm Beach Gardens, FL, USA, pp. 101–106.

Lewis III, R.R., 1990. Creation and restoration of coastal plain wetlands in Florida. In: Kusler, J.A., Kentula, M.E. (Eds.), Wetland Creation and Restoration: The Status of the Science. Island Press, Washington, DC, USA, pp. 73–101.

List, J., Sallenger Jr., A., Hansen, M., Jaffe, B., 1997. Accelerated relative sea-level rise and rapid coastal erosion: testing a causal relationship for the Louisiana barrier islands. Mar. Geol. 140, 347–365.

Lovelock, C.E., Ellison, J.C., 2007. Vulnerability of mangroves and tidal wetlands of the Great Barrier Reef to climate change. In: Johnson, J.E., Marshall, P.A. (Eds.), Climate Change and the Great Barrier Reef: A Vulnerability Assessment. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia, pp. 237–269.

McKee, K., 1993. Soil physiochemical patterns and mangrove species distribution-reciprocal effects? J. Ecol. 81, 477–487.

McKee, K.L., Cahoon, D.R., Feller, I., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Global Ecol. Biogeogr. 16, 545–556.

McKee, K.L., Feller, I.C., Popp, M., Wanek, W., 2002. Mangrove isotopoic (delta 15N and delta 13C) fractionaries across a nitrogen vs. phosphorous limitation gradient. Ecology 83, 1065–1075.

McLeod, E., Salm, R., 2006. Managing Mangroves for Resilience to Climate Change. IUCN, Gland, Switzerland.

Meehl, G.A., Tebaldi, C., Nychka, D., 2004. Changes in frost days in simulations of twenty-first century climate. Clim. Dynam. 23, 495–511.

Middleton, B.A., McKee, K.L., 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J. Ecol. 89, 818–828.

Mimura, N., Nunn, P., 1998. Trends of beach erosion and shoreline protection in rural Fiji. J. Coast. Res. 14, 37–46.

Mullane, R., Suzuki, D., 1997. Beach Management Plan for Maui. University of Hawaii Sea Grant Extension Service and County of Maui Planning Department, Maui, HI, USA.

Mumby, P., Edwards, A., Arlas-Gonzalez, J., Lindeman, K., Blackwell, P., Gall, A., Gorczynska, M., Harbone, A., Pescod, C., Renken, H., Wabnitz, C., Llewellyn, G., 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427, 533–536.

Mydlarz, L.D., Jones, L.E., Harvell, C.D., 2006. Innate immunity, environmental drivers, and disease ecology of marine and freshwater invertebrates. Annu. Rev. Ecol. Syst. 37, 251–288.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Naidoo, G., 1990. Effects of nitrate, ammonium and salinity on growth of the mangrove *Bruguiera gymnorrhiza* (L.) Lam. Aquat. Bot. 38, 209–219.

Naidoo, G., 1985. Effects of waterlogging and salinity on plant–water relations and on the accumulation of solutes in three mangrove species. Aquat. Bot. 22, 133–143.

Naidoo, G., 1983. Effects of flooding on leaf water potential and stomatal resistance in *Bruguiera gymnorrhiza*. New Phytol. 93, 369–373.

Nichols, R., Hoozemans, F., Marchand, M., 1999. Increasing flood risk and wetland losses due to sea-level rise: regional and global analyses. Global Environ. Change 9, S69–S87.

Nystrom, M., Folke, C., 2001. Spatial resilience of coral reefs. Ecosystems 4, 406–417.

Odum, E.P., 1989. Ecology and Our Endangered Life-Support Systems. Sinauer Associates Inc., Sunderland, USA.

Palumbi, S.R., Grabowsky, G., Duda, T., Geyer, L., Tachino, N., 1997. Speciation and population genetic structure in tropical Pacific sea urchins. Evolution 51, 1506–1517.

Pilkey, O.H., Cooper, J.A., 2004. Society and sea level rise. Science 303, 1781–1782.

Piou, C., Feller, I.C., Berger, U., Chi, F., 2006. Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane. Biotropica 38, 365–372.

Pizzuto, J.E., Schwendt, A.E., 1997. Mathematical modeling of autocompaction of a Holocene transgressive valley-fill deposit, Wolfe Glade, Delaware. Geology 25, 57–60.

Primavera, J., 1997. Socio-economic impacts of shrimp culture. Aquacult. Resour. 28, 815–827.

Ramsar Secretariat, 2001. Wetland Values and Functions: Climate Change Mitigation. Gland, Switzerland.

Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Ruckelshaus, M., Warner, R.R., 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecol. Appl. 13, S215–S228.

Roberts, C., Halpern, B., Palumbi, S., Warner, R., 2001. Designing marine reserve networks: why small, isolated protected areas are not enough. Conserv. Biol. Pract. 2, 10–17.

Rogers, K., Saintilan, N., Heijnis, H., 2005a. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence, and sea level rise. Estuaries 28, 551–559.

Rogers, K., Saintilan, N., Cahoon, D.R., 2005b. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. Wetl. Ecol. Manage. 13, 587–598.

Saad, S., Husain, M.L., Asano, T., 1999. Sediment accretion of a tropical estuarine mangrove: Kemarnan, Terengganu, Malaysia. Tropics 8, 257–266.

Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetl. Ecol. Manage. 9, 409–420.

Salm, R.V., Done, T., McLeod, E., 2006. Marine protected area planning in a changing climate. In: Phinney, J.T., Hoegh-Guldberg, O., Kleypas, J., S-kirving, W., Strong, A. (Eds.), Coral Reefs and Climate Change: Science and Management. American Geophysical Union, Washington, DC, pp. 207–221.

Scheffer, M., Carpenter, S., Foley, J., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Semeniuk, V., 1994. Predicting the effect of sea-level rise on mangroves in northwestern Australia. J. Coast. Res. 10, 1050–1076.

Shaw, J., Ceman, J., 1999. Salt-marsh aggradation in response to late-Holocene sea-level rise at Amherst Point, Nova Scotia, Canada. n 9, 439–451.

Sherman, R.E., Fahey, T.J., Martinez, P., 2001. Hurricane impacts on a mangrove forest in the Dominican Republic, damage patterns and early recovery. Biotropica 33, 393–408.

Smith III, T.J., Robblee, M.B., Wanless, H.R., Doyle, T.W., 1994. Mangroves, hurricanes and lightning strikes. BioScience 44, 256–262.

Snedaker, S., 1995. Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. Hydrobiologia 295, 43–49.

Snedaker, S., 1993. Impact on mangroves. In: Maul, G.A. (Ed.), Climate Change in the Intra-American Seas: Implications of Future Climate Change on the Ecosystems and Socio-economic Structure of the Marine and Coastal Regimes of the Caribbean Sea, Gulf of Mexico, Bahamas and N. E. Coast of South America. Edward Arnold, London, pp. 282–305.

Solomon, S., Qin, D., Manning, M., Alley, R.B., Berntsen, T., Bindoff, N.L., Chen, Z., Chidthaisong, A., Gregory, J.M., Hegerl, G.C., Heimann, M., Hewitson, B., Hoskins, B.J., Joos, F., Jouzel, J., Kattsov, V., Lohmann, U., Matsuno, T., Molina, M., Nicholls, N., Overpeck, J., Raga, G., Ramaswamy, V., Ren, J., Rusticucci, M., Somerville, R., Stocker, T.F., Whetton, P., Wood, R.A., Wratt, D., 2007. Technical summary. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Stewart, R.R., Noyce, T., Possingham, H.P., 2003. Opportunity cost of ad hoc marine reserve 5 design decisions: an example from South Australia. Mar. Ecol. Prog. Ser. 253, 25–38.

Tait, J.F., Griggs, G., 1990. Beach response to the presence of a seawall. Shore Beach 58, 11–28.

Thom, B.G., 1984. Coastal landforms and geomorphic processes. In: Snedaker, S.C., Snedaker, J.G. (Eds.), The Mangrove Ecosystem: Research Methods. UNESCO, Paris, pp. 3–15.

Thomas, R., Rignot, E., Casassa, G., Kanagaratnam, P., Acuna, C., Akins, T., Brecher, H., Frederick, E., Gogineni, P., Krabill, W., Manizade, S., Ramamoorthy, H., Rivera, A., Russell, R., Sonntag, J., Swift, R., Yungel, J., Zwally, J., 2004. Accelerated sea-level rise from West Antarctica. Science 306, 255–258.

Titus, J.G., 1991. Greenhouse effect and coastal wetland policy: how Americans could abandon an area the size of Massachusetts at minimum cost. Environ. Manage. 15, 39–58.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge, UK.

Tompkins, E.L., Adger, N.W., 2004. Does adaptive management of natural resources enhance resilience to climate change? Ecol. Soc. 19, 10.

Turner, B.L., Kasperson, R., Matsone, P., McCarthy, J., Corell, R., Christensene, L., Eckley, N., Kasperson, J., Luerse, A., Martello, M., Polsky, C., Pulsipher, A., Schiller, A., 2003. A framework for vulnerability analysis in sustainability science. PNAS Early Edition 100, 8074–8079.

UNEP, 1994. Assessment and monitoring of climate change impacts on mangrove ecosystems. UNEP Regional Seas Reports and Studies No. 154. Regional Seas Programme, Nairobi, Kenya.

Valiela, I., Bowen, J., York, J., 2001. Mangrove forests: one of the world's threatened major tropical environments. Bioscience 51, 807–815.

Vavrus, S.J., Walsh, J.E., Chapman, W.L., Portis, D., 2006. The behavior of extreme cold air outbreaks under greenhouse warming. Int. J. Climatol. 26, 1133–1147.

Wakushima, S., Kuraishi, S., Sakurai, N., Supappibul, K., Siripatanadilok, S., 1994a. Stable soil pH of Thai mangroves in dry and rainy seasons and its relation to zonal distribution of mangroves. J. Plant Res. 107, 47–52.

Wakushima, S., Kuraishi, S., Sakurai, N., 1994b. Soil salinity and pH in Japanese mangrove forests and growth of cultivated mangrove plants in different soil conditions. J. Plant Res. 107, 39–46.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Wells, S., 2006. Establishing National and Regional Systems of MPAs—A Review of Progress With Lessons Learned. UNEP World Conservation Monitoring Centre, UNEP Regional Seas Programme, ICRAN, IUCN/WCPA – Marine.

Wells, S., Ravilous, C., Corcoran, E., 2006. In the Front Line: Shoreline Protection and Other Ecosystem Services from Mangroves and Coral Reefs. United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, UK.

Whelan, K.R.T., Smith III, T.J., Cahoon, D.R., Lynch, J.C., Anderson, G.H., 2005. Groundwater control of mangrove surface elevation: shrink–swell of mangrove soils varies with depth. Estuaries 28, 833–843.

Wilton, K., 2002. Coastal wetland habitat dynamics in selected New South Wales estuaries, vol. 1. Ph.D. Thesis. Australian Catholic University, Fitzroy, Australia.

Woodroffe, C., 2002. Coasts: Form, Process and Evolution. Cambridge University Press, Cambridge, UK.

Woodroffe, C.D., 1995. Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. Earth Surf. Proc. Land. 20, 65–85.

Woodroffe, C.D., 1992. Mangrove sediments and geomorphology. In: Alongi, D., Robertson, A. (Eds.), Tropical Mangrove Ecosystems. Coastal and Estuarine Studies. American Geophysical Union, Washington, DC, pp. 7–41.

Woodroffe, C.D., 1990. The impact of sea-level rise on mangrove shorelines. Prog. Phys. Geogr. 14, 483–520.

Woodroffe, C.D., 1987. Pacific island mangroves: distributions and environmental settings. Pacific Sci. 41, 166–185.

Woodroffe, C.D., Grime, D., 1999. Storm impact and evolution of a mangrove-fringed chenier plain, Shoal Bay, Darwin, Australia. Mar. Geol. 159, 303–321.

Woodroffe, C.D., Thom, B.G., Chappell, J., 1985. Development of widespread mangrove swamps in mid-Holocene times in northern Australia. Nature 317, 711–713.

Woodroffe, C.D., Grindrod, J., 1991. Mangrove biogeography: the role of quaternary environmental and sea-level change. J. Biogeogr. 18, 479–492.

Woodworth, P.L., Blackman, D.L., 2004. Evidence for systematic changes in extreme high waters since the mid-1970s. J. Climate 17, 1190–1197.

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Review

Functionality of restored mangroves: A review

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ABSTRACT

Widespread mangrove degradation coupled with the increasing awareness of the importance of these coastal forests have spurred many attempts to restore mangroves but without concomitant assessment of recovery (or otherwise) at the ecosystem level in many areas. This paper reviews literature on the recovery of restored mangrove ecosystems using relevant functional indicators. While stand structure in mangrove stands is dependent on age, site conditions and silvicultural management, published data indicates that stem densities are higher in restored mangroves than comparable natural stands; the converse is true for basal area. Biomass increment rates have been found to be higher in younger stands than older stands (e.g. 12 t ha^{-1} $year^{-1}$ for a 12 years plantation compared to 5.1 t ha^{-1} $year^{-1}$ for a 80-year-old plantation). Disparities in patterns of tree species recruitment into the restored stands have been observed with some stands having linear recruitment rates with time (hence enhancing stand complexity), while some older stands completely lacked the understorey. Biodiversity assessments suggest that some fauna species are more responsive to mangrove degradation (e.g. herbivorous crabs and mollusks in general), and thus mangrove restoration encourages the return of such species, in some cases to levels equivalent to those in comparable natural stands. The paper finally recommends various mangrove restoration pathways in a functional framework dependent on site conditions and emphasizes community involvement and ecosystem level monitoring as integral components of restoration projects.

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Table 1
Yield table data for mangrove plantations at Gazi

Parameters	Utilization classes (cm)				
	<4.0	4.1–6.0	6.1–9.0	9.1–13	Total
Stems ha^{-1}	559	1586	2392	327	4864
Merchantable volume[a] (m^3 ha^{-1})	1.56	11.63	37.81	9.7	60.71
Un-merchantable volume (m^3 ha^{-1})					43.09
Standing biomass (t ha^{-1})	2.35	18.55	66.36	19.39	106.66
Below ground biomass (t ha^{-1})					24.89

[a] Volume equation used is y, $4a^2 \times 10^{-10} + 3a \times 10^{-5} + 2a \times 10^{-5}$, where y is the stem volume, and $a = D_{130}^2 H$ (*source*: Kairo et al., 2008).

1. Introduction

Towards the end of the twentieth century, scientific concern began to focus on the unprecedented loss of naturally occurring mangroves ecosystems around the world (Walsh et al., 1975). In 1983, UNDP and UNESCO established a regional project concerned with the value of mangrove ecosystems in Asia and the Pacific.

This international initiative led to an increased appreciation of the value of mangroves and a subsequent upsurge of mangrove restoration efforts (Field, 1996; Kairo et al., 2001). Some of the objectives driving early mangrove reforestation efforts include: wood production for timber, poles and fuel wood; fisheries productivity; coastal protection against storms, and legislative compliance (Ong, 1982; Field, 1996; Saenger, 2002). The rationale for mangrove restoration has changed very slowly over the years from just silviculture to recognition of mangroves as a diverse resource. The term 'restore' is taken to mean the creation of a sustainable functioning mangrove ecosystem that may or may not resemble its precursor at the very same site.

The early attempts at mangrove restoration met with mixed results with some being successful, while others were doomed from the start (Field, 1996; Erftemeijer and Lewis, 1999). Most of these attempts were not based on well-understood ecological principles and well-defined aims.

In more recent times, attention has turned to the ecological processes present in natural and restored mangrove systems (Alongi, 2002; Saenger, 2002; Lewis, 2005; McKee and Faulkner, 2000). The relationship between the restored mangrove ecosystem and adjoining ecosystems, such as salt marsh (Santilan and Hasimoto, 1999) and seagrass beds (Hogarth, 2007) has also been a focus of attention. A consensus has emerged that an understanding of mangrove hydrology is most important for successful restoration (Wolanski et al., 1992).

Ellison (2000) did a comprehensive review on mangrove restoration examining goals of existing restoration projects, and whether these goals address the full range of biological diversity and ecological processes of mangrove ecosystems. He pointed out that the focus on silviculture remained the primary objective of mangrove restoration and that few species had been involved and indicated that adequate data exists to enable successful mangrove restoration but emphasized that assessment of structural and functional characteristics of restored mangroves is imperative. This paper takes Ellison's review (Ellison, 2000) further and presents a comprehensive review of the data available on the functionality of restored mangrove ecosystems in respect to a number of functional indicators: vegetation structure, natural regeneration, productivity, nutrient recycling to conservation of inherent biodiversity and socio-economic valuation. Finally, it looks at the constraints and opportunities for successful mangrove restoration. Within the context of this review, functionality is used to refer to the ability of restored mangroves to process nutrients and organic matter, trap sediments, provide food and habitat for animals, protect shorelines, provide plant products and a scenic environment, in a similar fashion to natural mangrove forests. These aspects are often referred to as the goods and services that mangroves can provide (Walters et al., 2008).

2. Forest structure, biomass and regeneration

2.1. Structure, regeneration and biomass of restored mangroves

Most of the studies on mangrove forest structure and regeneration have focused on natural stands (e.g. Cole et al., 1999; Kairo et al., 2002); with relatively few references on reforested stands such as in the Matang forest reserve (Putz and Chan, 1986; Ong et al., 1995); as well as Ranong in Thailand (FAO, 1985; Choudhury, 1997) and Sundarban in India (Hussain, 1995; Choudhury, 1997). Apart from studies by Bosire et al. (2003, 2006), and Kairo et al. (2008), at Gazi bay in Kenya, little is known about structural development of replanted mangroves in Africa.

Analysis of stand table data from a 12 years old (Table 1) *Rhizophora mucronata* Lamk plantation in Kenya indicate that reforested plots have the potential of yielding 4864 stems ha^{-1} (much higher than the stem density in a natural stand of the same species at the same site of 1796 stems ha^{-1}; Bosire et al., 2006), with a standing biomass and merchantable volume of 106.7 t ha^{-1} and 60.7 m^3 ha^{-1}, respectively (Kairo et al., 2008). This standing biomass is much lower than the 240 t ha^{-1} observed in a nearby *R. mucronata* natural stand (Slim et al., 1997). The root biomass value in replanted *R. mucronata* was 24.9 ± 11.4 t ha^{-1}; which is 19% of the total plant biomass (Kairo et al., 2008). A review of literature on biomass studies indicates that root biomass values vary from one study to another depending on the method used (e.g. Vogt et al., 1998) and the data obtained in Kenya is comparable to ranges observed for *Rhizophora* studies in Thailand (Alongi and Dixon, 2000).

The biomass accumulation rate for the 12-year-old *Rhizophora* plantation in Kenya was estimated at 12 t ha^{-1} year^{-1} (Kairo et al., 2008). This value is higher than the 5.1 t ha^{-1} year^{-1} reported for an 80-year-old natural plantation of *Rhizophora apiculata* Bl. in Malaysia (Putz and Chan, 1986). In Matang mangrove forest, Ong et al. (1995) reported aboveground biomass increment of 24.5 t ha^{-1} year^{-1} (and 34 t ha^{-1} year^{-1} when belowground biomass was included) for 20-year-old plantation. It is logical to conclude that biomass accumulation rate is influenced by age, species, management system applied, as well climate.

The mean canopy height for the 12-year-old *Rhizophora* plantation in Kenya was 8.4 ± 1.1 m (range: 3.0–11.0 m) with a mean stem diameter of 6.2 ± 1.9 cm (range: 2.5–12.4 cm). These values are within the range reported for *Rhizophora* plantations in South East Asia (see, e.g. Srivasatava et al., 1988; FAO, 1994). Based on growth data, the mean annual increment (MAI) in height and diameter (DBH) for the *Rhizophora* plantation in Kenya were 0.71 m and 0.53 cm, respectively. These figures are within the range of published mangrove growth rates (7–12 m for height, and 5–15 cm for diameter) in Asia and Pacific (Watson, 1931; Durant, 1941; Putz and Chan, 1986; UNDP/UNESCO, 1991; Devoe and Cole, 1998;

Saenger, 2002). The basal area for 12-year-old *R. mucronata* was 16.5 m^2 ha^{-1}, which was lower than that of a natural stand of the same species (e.g. Bosire et al., 2006). This is expected since, despite having a higher stand density than a natural stand, most of the stems were of smaller size classes. A decline in stand density and an increase in basal area are typical for a developing forest (Twilley, 1995).

2.2. Composition and pattern of natural regeneration

Seedling recruitment and survivorship principally drives population growth (Burns and Ogden, 1985; Krauss et al., 2008) and thus determines the quality of the crop and productivity of forest stands (Srivastava and Bal, 1984). This becomes even more critical in restored mangrove sites where for economic reasons, many plantations tend to be monocultures (Walters, 2000; Bosire et al., 2006) Therefore evaluation of the regeneration potential of a stand, in terms of seedling density, composition, sizes and the possibility of recruitment into the adult canopy.

When conducting natural regeneration sampling in mangroves, newly recruited juveniles measuring 30 cm and below are referred to as 'potential regeneration. Individuals greater than 30 cm and higher are termed 'established regeneration, whereas those greater than 150 cm are saplings or young trees. For adequate natural regeneration a minimum of 2500 well-distributed seedlings per hectare has been proposed (Srivastava and Bal, 1984).

The recruitment rate of saplings has been found to be increasing with age in one *R. mucronata* Lamk. plantation in Kenya (Fig. 1). The densities observed in this plantation are however, much lower than those observed in a comparable conspecific natural stand at the same location (see, e.g. Kairo et al., 2002; Bosire et al., 2006), suggesting age may be a critical factor in determining the level of natural regeneration. In subsequent assessments, the canopy species has dominated the juvenile density in contrast to *Bruguiera gymnorrhiza* (L.) Lamk. dominance at earlier stages of forest development (Bosire et al., 2003). Some non-planted mangrove species have also been recruited into the adult canopy of the same plantation hence enhancing stand complexity (Bosire et al., 2003, 2006) contrary to a *S. alba* replanted stand of the same age where species encountered as juveniles experienced 100% mortality and thus none were observed in the adult canopy. This mortality of non-conspecific species was attributed to tidal submergence and barnacle infestation typical of this inundation class (Bosire et al., 2006). Contrary to observations in Kenya, Walters (2000) found no post-planting sapling recruitment in 50–60-year-old *R. mucronata* plantations in the Philippines probably due to periodic removal (weeding) of non-planted species by locals and in some plantations no actual natural colonization at all.

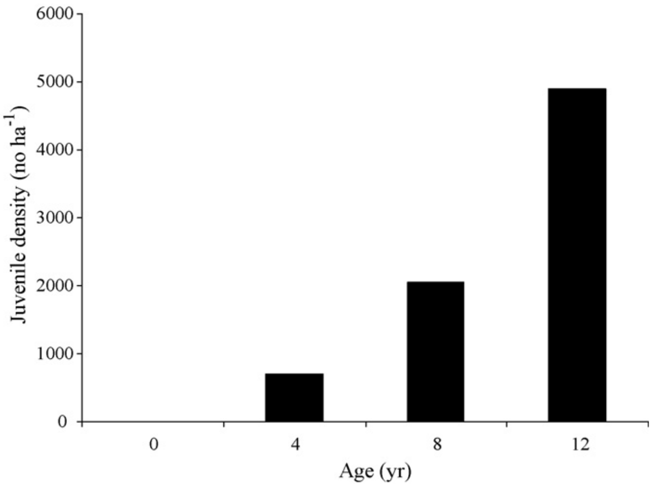

Fig. 1. Sapling recruitment over time in a *R. mucronata* plantation in Kenya.

3. Biodiversity in restored mangroves

While mangrove associated fauna play such a significant role in the functioning of the ecosystem (Kristensen, 2007; Lee, 2007; Cannicci et al., 2008; Kristensen et al., 2008; Nagelkerken et al., 2008) and thus can be a useful indicator of the state of managed mangroves, silvicultural management more often than not ignores assessing this component (Ellison, 2007). This section will highlight some trends in recolonization of epibiotic, macrobenthic and sediment-infauna communities and also look at distribution patterns for benthic macrofauna, fish and shrimp in replanted stands across the world, with focus on species richness and community assemblages.

3.1. Epibiotic and epibenthic communities

It is important to investigate to what extent mangrove restoration does support faunal recolonisation. In Thailand, crab diversity at some of the replanted sites was higher than at an upper shore natural mangrove site, and both biomass and crab numbers were consistently higher in the replanted sites (Macintosh et al., 2002). However, the natural site was characterized by large numbers of sesarmid crabs. Differences in the crab diversity in Thailand were reported to relate to inundation zone and differences in the mangrove species present in the replanted sites (Macintosh et al., 2002). However, in Qatar (Al-Khayat and Jones, 1999) found lower species richness of crabs in plantations compared to natural habitats of *Avicennia marina* (Forssk.) Vierh.

In Kenya, reforested stands of *R. mucronata* and *A. marina* had higher crab densities than their natural references (Bosire et al., 2004) but with similar species diversity and crab species composition compared to bare controls with similar site history. More sesarmid species were observed in the reforested stands (similar to the natural references) than the bare controls. Since sesarmids are thought to be key stone species with respect to nutrient recycling (Kristensen et al., 2008; Cannicci et al., 2008), they therefore seem more responsive to ecosystem degradation or restoration. In the Philippines the relative abundance of the exploited mud crab *Scylla olivacea* (Herbst) compared to two other non-commercial species was used to separate the effects of habitat from fishing pressure and recruitment limitation. A comparison of mud crab populations in replanted, natural and degraded sites in the Philippines suggested that 16 years old replanted *Rhizophora* spp. can support densities of mud crabs equivalent to that of natural mixed species mangroves (Walton et al., 2007).

Mollusc diversity showed similar patterns to that of crabs in both previously mentioned studies in Qatar and Thailand, while in Kenya, no mollusks were observed in the bare site of *Sonneratia alba* J. Smith with the reforested site and natural reference having similar species composition, density and diversity. The lack of mollusks in the bare site emphasizes the consequences of mangrove degradation on biodiversity, while similarities among the replanted site and natural reference suggest the potential of mangrove restoration in enhancing faunal recolonisation.

Studies of epibiotic communities in Kenya (Crona et al., 2006) compared natural stands with two 8-year-old *Sonneratia alba* plantations; an integrated plantation (a reforested stand originally degraded site but with some remaining mangroves) and a matrix plantation (a reforested stand which was originally clear-felled). The study showed a decreasing trend of similarity with natural stands when comparing macroalgal assemblages of an integrated plantation, a matrix plantation and a clear felled area, in this order.

Both algal diversity and root fouling faunal cover and biomass were lower in the matrix plantation compared to the integrated plantation and natural stand which was attributed to lower root area, in combination with longer inundation times and larval behaviour and longevity of poriferans and barnacles, which may affect recruitment patterns.

3.2. Sediment-infauna

Sediment-infauna communities showed patterns similar to those described above. Lower diversity of taxa was observed in planted versus natural sites in Qatar with the picture being less clear in Thailand. Infaunal studies in the Matang mangroves in Malaysia suggested that 2-year-old planted mangroves had the greatest biomass and species number followed by the mature and 15-year-old stand, although species diversity was highest in the mature site and lowest in the 2-year-old site (Sasekumar and Chong, 1998). In Kenya, bare sites of *A. marina*, *R. mucronata* and *S. alba* had the lowest infauna densities and taxa richness compared to respective replanted sites with conspecific natural references having the highest densities. Taxa richness and composition were similar among respective replanted and natural sites (Bosire et al., 2004), suggesting successful fauna recolonisation following mangrove restoration.

3.3. Vagile fauna–fish and shrimp

Mangroves support nursery functions for many juvenile fish and shrimp species, many of which are highly important commercially (Lewis et al., 1985; Rönnbäck et al., 1999; Nagelkerken et al., 2008). Juvenile fish and shrimp species are known to be dependent on structural complexity for refuge (Primavera, 1997) and therefore the intensity of this function is linked to the type of mangrove in focus (Ewel et al., 1998; Rönnbäck et al., 2001). Studies of vagile fauna in replanted mangroves of varying ages and species composition showed variable patterns. In Qatar, lower diversity of both juvenile and adult fish was observed in plantations compared to natural stands of *A. marina* (Al-Khayat and Jones, 1999). Studies comparing fish and shrimp density between natural stands of *R. apiculata* Bl., *Avicennia officinalis* L., *A. marina* and a single replanted *R. apiculata* stand (5–6 years old) in the Philippines indicated that density and biomass were primarily influenced by tidal height and mangrove species (Rönnbäck et al., 1999). In *S. alba* plantations in Kenya, there were strong seasonal fluctuations for juvenile fish, showing temporal patterns to be a potentially stronger influence on fish assemblages than type of plantation or presence of fringing mangroves (Crona and Rönnbäck, 2007). However, the spatial scale of observation is likely a much stronger factor affecting biodiversity studies of plantations for vagile fauna compared to less mobile communities described above. Since most studied plantations are small in size, the effect of plantations on fish distribution patterns therefore remains largely unknown. The same is true for juvenile shrimps. In Kenya lower species richness was observed in a matrix plantation of *S. alba*, and in adjacent clear felled areas one species, *Penaeus japonicus* (Bate), dominated the community (Crona and Rönnbäck, 2005). Natural forests had higher root complexity and also higher abundances and more even distribution of shrimp species in terms of species composition. Similarly, in the Philippines, higher abundances of juvenile shrimp in a planted *R. apiculata* site were seemingly related to higher structural root complexity, although more inland stands of mature *Avicennia* spp. and *Rhizophora* spp. showed no such differences and had equally high densities as the near-shore *Rhizophora* spp. (Rönnbäck et al., 1999).

Few studies exist on trends in biodiversity in restored mangroves, and the range in age, species and inundation class of restored sites makes generalizations hard. However, the co-occurrence of many animal species in both restored and comparable natural forests suggest recovery of the former sites. Lewis (1992) in reviewing both tidal marsh and mangrove restoration projects in the United States noted that the recovery of fish populations back to similar species composition and density as reference sites has been accomplished within 5 years. To optimize fish habitat in mangrove restoration projects, Lewis and Gilmore (2007) have recommended restoration of tidal creeks to provide access and low tide refuge for mobile nekton.

Although the results reviewed in this section are quite variable most likely due sampling design and intensity, in most cases they suggest remarkable recovery of biodiversity in restored mangroves. It is also apparent that mangrove degradation causes not only a general decline in species richness and/or diversity, but also functional shifts as sets of species with particular traits are replaced. Some higher order groups have also been found to be more sensitive to mangrove degradation, e.g. sesarmid crabs and mollusks. This suggests that while abundance and diversity are important measures of biodiversity, species composition as an analogue to functional diversity, may be an additional, more objective and distinct index of measuring faunal recovery in restored mangroves. To make data obtained from various locations comparable, it will be necessary for teams involved in mangrove restoration ecology to agree on standard approaches to measure recovery of biodiversity. Currently these do not exist.

4. Socio-economics of mangrove restoration

The socio-economic importance of natural mangrove goods and services has been documented repeatedly (Ruitenbeek, 1994; Walters, 1997; Adger et al., 2001; Barbier, 2006; Walters et al., 2008), but can restored mangroves generate income similar to that of natural mangroves? To date there have been insufficient studies in replanted mangroves to be sure and comparisons are further complicated by the diversity in productivity of natural mangrove habitats.

Mangroves were initially planted in order to generate income from timber. At Matang in Malaysia one of the best-managed mangrove plantations can be found (Gong and Ong, 1995). Here, 17.4 t ha^{-1} year^{-1} of mangrove wood is harvested sustainably over a 30-year cycle (Gan, 1995). A similar study in Java suggested that a 7-year-old *R. mucronata* plantation had a standing trunk and branch biomass of 74 t ha^{-1}, and a production of 10.6 t ha^{-1} year^{-1} (Sukardjo and Yamada, 1992).

Governments are increasingly aware of the nursery and fisheries enhancement function of mangroves. In the Mekong Delta, Soc Trang province, Vietnam, extensive planting of *Rhizophora* species was used as a coastal protection measure. Recent studies here in a 7 ha area reforested in 1995 with *R. apiculata* suggested an annual harvest rate of fish and crustaceans of 143 kg^{-1} ha^{-1} year^{-1} valued at USD 363 ha^{-1} year^{-1} (Walton and Le Vay, unpublished, 2006).

Recently a questionnaire-based socio-economic study on the Buswang replanted mangroves in the Philippines suggested the mangrove was directly benefiting local incomes in the region of USD 564–2316 ha^{-1} year^{-1} (Walton et al., 2006a). Contributing to the annual income are mollusc, crustacean and fish catches from within the mangroves (294 kg ha^{-1} worth USD 213 ha^{-1}), tourism (USD 41 ha^{-1}), timber (USD 60 ha^{-1}) and an estimate of contribution of these mangroves to near-shore coastal mangrove associated fish (10% to 276 kg ha^{-1} worth USD 250 ha^{-1} to 80% to 2204 kg ha^{-1} worth USD 2002 ha^{-1}). The increase in interest in carbon credits could in the future also raise an additional income of USD 163–198 ha^{-1} year^{-1} (Walton et al., 2006a). These fisheries values compare favourably with those from natural mangroves that are estimated to support fisheries valued at between USD 750–11,280 ha^{-1} $year^{-1}$ (Rönnbäck, 1999).

Other indirect benefits such as coastal protection and non-use values (option, bequest and existence values) are more difficult to gauge. Since the establishment of the Buswang mangrove, storm surge damage and coastal erosion has been negligible, but in some other countries around the Indian Ocean, cases about storm-associated costs have been documented (cf. Gilman et al., 2008). In India for instance, monetary losses due to repair and reconstruction costs of personal property (incl. livestock and agricultural products) ranged between 32 USD per household in mangrove-protected villages to 154 USD per household in villages that were not protected by mangroves (Badola and Hussain, 2005). In the past, replacement costs have been used to estimate coastal protection value. However replacement cost associated with constructed breakwaters generally overestimate the value. As such this should be modified by the area that requires coastal protection estimated as USD 3679 ha^{-1} $year^{-1}$ (Sathirathai and Barbier, 2001). Other indirect benefits include accretion of agricultural land. In the Sundarbans, Bangladesh, the planting of 150,000 ha of mixed mangrove species has enhanced the deposition of sediments to such an extent that the elevation of 60,000 ha is no longer suitable for mangrove, and can be used for agriculture worth US$ 800 ha^{-1} $year^{-1}$ (Saenger and Siddiqi, 1993). However, it remains to be seen to which extent novel functions gained, such as from agriculture, outweigh their possibly adverse ecological impacts on the mangrove.

While the total extent of the economic benefit of restored mangroves is as yet unclear, the initial planting costs are a major factor in preventing more community based replanting efforts. In the Philippines, initial costs are estimated to be USD 204 ha^{-1} using volunteers (Walton et al., 2006a). However mangrove restoration cost estimates for the United States of America ranged between 225 and 216,000 USD ha^{-1} (Lewis, 2005). These costs thus vary very widely depending on differential labour costs (dependent on GNP of the country in question (Brander et al., 2006), site conditions and thus the effort in terms of labour required for hydrological restoration and removal of debris and weeds among other factors, and planting material types where replanting is necessary. Grant-based aid and elimination of ownership doubts through community stewardship schemes could significantly boost mangrove replanting programs around the world.

5. Opportunities and constraints to mangrove forest restoration

Mangrove forest ecosystems currently cover an estimated 14.7 million ha of the tropical shorelines of the world (Wilkie and Fortuna, 2003). This represents a decline from 19.8 million ha in 1980 and 15.9 million ha in 1990. These losses represent about 2% $year^{-1}$ between 1980 and 1990, and 1% $year^{-1}$ between 1990 and 2000. Therefore achieving no-net-loss of mangroves worldwide would require the successful restoration of approximately 150,000 ha $year^{-1}$, unless all major losses of mangroves ceased. Increasing the total area of mangroves worldwide would require an even larger scale effort.

Recently, Duke et al. (2007) sounded once more the alarm bell and indicated that a world without mangroves is a realistic forecast if the destruction of mangrove ecosystems continues. Examples of documented losses include combined losses in the Philippines, Thailand, Vietnam and Malaysia of 7.4 million ha of mangroves (Spalding et al., 1997). These figures emphasize the level of opportunities that exist to restore larger areas of mangroves such as mosquito control impoundments in Florida (Brockmeyer et al., 1997) (tens of thousands of ha), and abandoned shrimp aquaculture ponds in Southeast Asia (Stevenson et al., 1999; hundreds of thousands of ha), back to functional mangrove ecosystems.

However while great potential exists to reverse the loss of mangrove forests worldwide, most attempts to restore mangroves often fail completely, or fail to achieve the stated goals (Elster, 2000; Erftemeijer and Lewis, 1999; Lewis, 2000, 2005).

Restoration or rehabilitation may be recommended when an ecosystem has been altered to such an extent that it can no longer self-correct or self-renew. Under such conditions, processes of secondary succession or natural recovery are inhibited in some way. Secondary succession depends upon mangrove propagule availability. Lewis (2005) proposed a new term, “propagule limitation” to describe situations in which mangrove propagules may be limited in natural availability due to removal of mangroves by development, or hydrologic restrictions or blockages (i.e. dikes) which prevent natural waterborne transport of mangrove propagules to a restoration site. In Sri Lanka, such hydrographical alterations have resulted in a decrease in forest flooding frequency by >90% (Dahdouh-Guebas, 2001). Predation on natural propagules can also limit their availability and indicate that broadcasting of collected seeds or planting may be essential for successful restoration (Dahdouh-Guebas et al., 1997, 1998; Bosire et al., 2005b; Cannicci et al., 2008).

Restoration has, unfortunately, emphasized planting mangroves as the primary tool in restoration, rather than first assessing the causes for the loss of mangroves in an area, then assessing the natural recovery opportunities, and how to facilitate such efforts. Thus most mangrove restoration projects move immediately into planting of mangroves without determining why natural recovery has not occurred. There may even be a large capital investment in growing mangrove seedlings in a nursery before existing stress factors at a proposed restoration site are assessed. This often results in major failures of planting efforts (Elster, 2000; Erftemeijer and Lewis, 1999; Lewis, 2005). In addition, few restoration efforts are embedded in a larger framework that also considers the fate of the planted mangroves, in terms of stand structure and regeneration, return of biodiversity and recovery of other ecosystem processes (Dahdouh-Guebas and Koedam, 2002). Recently these questions are starting to be tackled in an integrated way in East-African restored mangrove sites (Bosire et al., 2003, 2004, 2005a,b; Crona and Rönnbäck, 2005; Bosire et al., 2006; Crona et al., 2006).

Although a number of papers discuss mangrove hydrology (Kjerfve, 1990; Wolanski et al., 1992; Furukawa et al., 1997), their focus has been on tidal and freshwater flows within the forests, and not the critical periods of inundation and dryness that govern the health of the forest. Kjerfve (1990) does discuss the importance of topography and argues that “...micro-topography controls the distribution of mangroves, and physical processes play a dominant role in the formation and functional maintenance of mangrove ecosystems...” The point of all of this is that flooding depth, duration and frequency are critical factors in the survival of both mangrove seedlings and mature trees (Thampanya et al., 2003; Bosire et al., 2006), and also determine many of the functional attributes, like crustacean and fish use of forests. Once established, mangroves can be further stressed if the tidal or freshwater hydrology is changed, for example by diking (Brockmeyer et al., 1997; Dahdouh-Guebas et al., 2000a,b, 2005). Both increased salinity due to reductions in freshwater availability, and flooding stress, increased hypoxic or anoxic conditions and free sulfide availability can kill existing stands of mangroves. However, also increases in freshwater availability may result in a shift in species composition which favours ecologically and economically inferior species (Dahdouh-Guebas et al., 2005). The consulted scientist should therefore pay attention to both ecological and socio-economic functions of the mangrove stand or the restoration site in question.

Ecological restoration of mangrove forests has only received attention very recently (Lewis, 2000). The wide range of project types previously considered to be restoration, as outlined in Field (1996, 1998), reflect the many aims of classic mangrove rehabilitation or management for direct natural resource production. As mentioned previously, these include planting monospecific stands of mangroves for future harvest as wood products. This is not ecological restoration as defined by Lewis (2005).

Because mangrove forests may recover without active restoration efforts, it has been recommended that restoration planning should first look at the potential existence of stresses such as blocked tidal inundation that might prevent secondary succession from occurring, and plan on removing that stress before attempting restoration (Hamilton and Snedaker, 1984; Cintron-Molero, 1992). The next step is to determine whether natural seedling recruitment is occurring once the stress has been removed. Assisted natural recovery through planting should only be considered if natural recovery is not occurring.

Lewis and Marshall (1997) first suggested six critical steps necessary to achieve ecological mangrove restoration, and these are discussed in more detail in Stevenson et al. (1999). The general approach is to emphasize careful examination of factors hindering natural regeneration restoration opportunities while avoiding emphasizing planting of mangroves (Turner and Lewis, 1997). These steps have been tested in training courses on mangrove restoration in the USA and India, and have been further modified to support site-specific ecological restoration. However, the steps above have hitherto ignored the human dimension as an important consideration in mangrove restoration projects. In this paper we therefore further develop these steps into a functional framework which incorporates the human dimension (Fig. 2).

Mangrove forests may recover without active restoration efforts. When natural regeneration fails and the process needs human intervention, an understanding of the autoecology and community ecology of the targeted mangrove species is necessary, i.e. its reproductive patterns, propagule dispersal, seedling establishment, zonation and hydrology (steps 1 and 2). With this understanding, an assessment of factors hampering successful secondary succession can be done (step 3), involving the local knowledge of communities depending on the mangroves (step 4), which will be relevant throughout the subsequent steps. The perceptions and expectations of the local community depending on the mangroves should be considered during mangrove planting (cf. Dahdouh-Guebas et al., 2006). Coastal populations in industrialized countries typically do not depend on mangroves for their daily livelihoods, but in the majority of mangrove countries (developing countries) they do. The concerns of the local people in terms of how dependent they are on the mangroves, which species preferences do they have, and which alternatives can be offered while the natural ecosystem is left to recover or a planted site is left to develop can be captured through socio-ecological surveys, which can then be integrated in the restoration exercise (Dahdouh-Guebas, 2008). The surveys can also yield fundamental social and economic drivers of deforestation, which are equally important to restoration as hydrology. More specifically, the perceived value among local users of the ecosystem goods and services provided by mangroves to their overall livelihoods is essential if socio-economic drivers of degradation are to be altered or decreased (Rönnbäck et al., 2007).

The socio-ecological information gathered from steps 3 and 4 is then used to select appropriate restoration sites (step 5), and the obstacles to successful natural regeneration removed (step 6). If conditions are favourable, this should allow natural revegetation (successful aided natural regeneration) of the site, which is more cost-effective than replanting. If natural revegetation fails despite all these interventions (cf. Dahdouh-Guebas and Koedam, 2008,

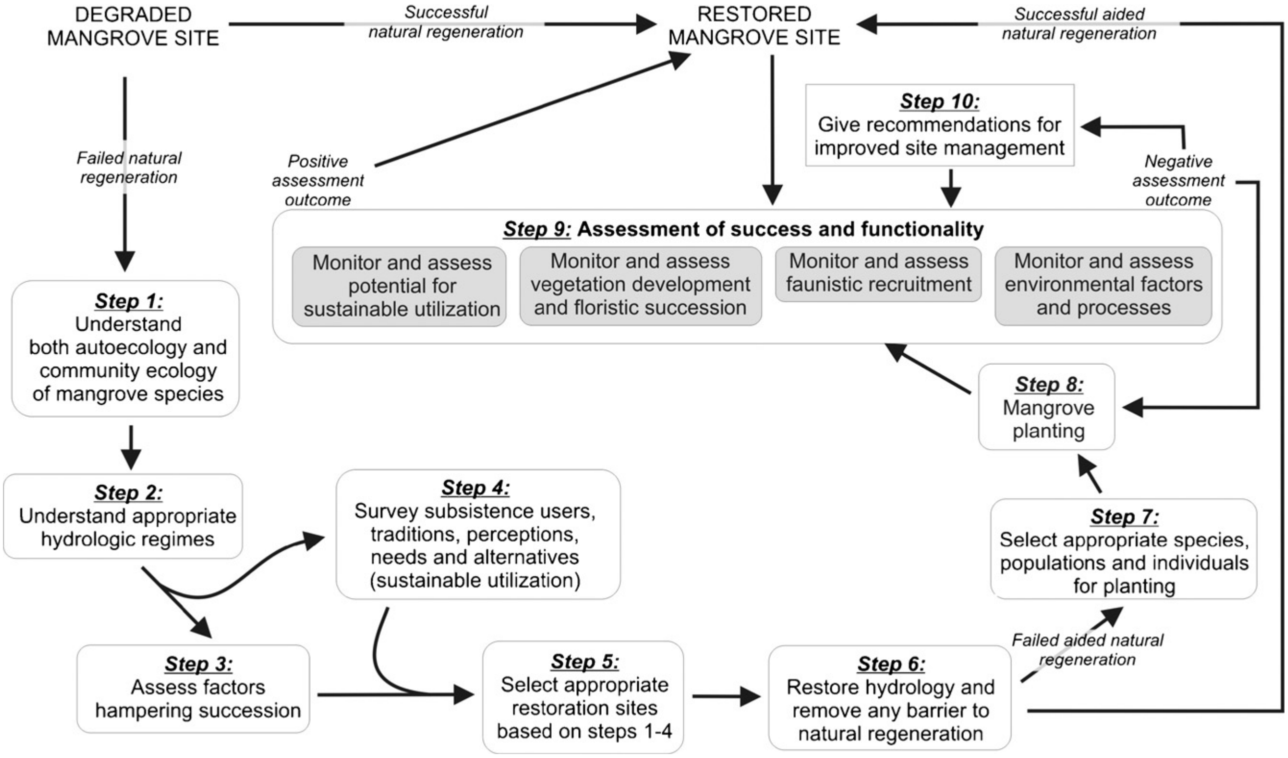

Fig. 2. A 10 steps scheme presenting possible mangrove restoration pathways depending on site conditions (modified after Stevenson et al., 1999; Bosire et al., 2006).

Fig. 1), then appropriate mangrove species, populations and individuals for planting (step 7) must be selected in view of genetic diversity (Triest, 2008), faunistic impacts (Cannicci et al., 2008) and individual performance (Komiyama et al., 2008) and mangrove replanting (step 8) becomes necessary to restore the degraded site. At regular intervals the replanting effort should be assessed for four different key factors in mangrove ecosystem functioning (step 9): the flora, the fauna, the environment and human subsistence use. When the assessment has a negative outcome, recommendations should be given for improved site management (step 10), which may have to be accompanied by extra planting. When the assessment has a positive outcome the site has restored, although further monitoring of the restored site can be undertaken as necessary.

The assessment of success of restoration is an essential step that is unfortunately backed up by few scientific papers (Walters, 2000; Macintosh et al., 2002; Bosire et al., 2004, 2006; Crona and Rönnbäck, 2005; Crona et al., 2006; Walton et al., 2006a,b; Lewis and Gilmore, 2007). We recommend that four assessment types are necessary as indicators of restoration success: development of the vegetation and floristic succession, faunistic recruitment, evolution of environmental factors and processes, and finally the potential for sustainable exploitation. The first three indicators can be started soon after the initiation of the natural recovery or plantation and can be repeated regularly (Bosire et al., 2006), whereas the last one is on a longer term of >10 or even >20 years. All of these can be assessed by using natural sites (references) under the same conditions on one hand, and to bare sites lacking mangroves on the other hand, as discussed in the preceding sections.

From the foregoing, it is clear that the two primary factors in designing a successful mangrove restoration project are habitat conditions (e.g. hydrology, herbivory and weed cover among others) as well as the participation of local communities from the onset of the restoration initiative. Community involvement is likely to increase the legitimacy of the restoration project and increase the likelihood of future sustainable use and compliance with regulatory measures to protect the developing stands of restored mangroves (Rönnbäck et al., 2007). Determination of appropriate hydrology (depth, duration and frequency of tidal flooding) of existing natural mangrove plant communities (a reference site) in the area in which you wish to do restoration is a critical factor. For instance, Vivian-Smith (2001) recommends the use of a reference tidal marsh for restoration planning and design. A common surrogate for costly tidal data gathering or modeling is the use of a tidal benchmark and survey of existing healthy mangroves. Similar topography is then established at the proposed restoration site, normal hydrology restored to a diked site, or tidal streams reestablished or created at damaged sites to ensure proper drainage, propagule dispersal and faunal access during tidal flooding.

A question that needs to be addressed in contemporary mangrove restoration projects is whether monospecific planting is appropriate in all situations. Considering that mixed species stands, even if dominated by few species, are common (e.g. mosaic mangrove stands in Sri Lanka, Dahdouh-Guebas et al., 2000a,b), one should consider the possibility that in some reforestation projects, monospecific planting may not be ideal, and even counter-advised. In the Philippines, an extensive area of monospecifically replanted *Rhizophora* spp. was lost due to an attack by tussock moth larvae (Walton et al., 2006b). Modelling vegetation development and individual interactions may be a helpful tool in the entire restoration framework (cf. Berger et al., 2008).

In summary, maintaining a no-net-loss of mangrove habitat worldwide will require very large scale restoration efforts which demand a common ecological engineering approach and application of the steps to successful restoration outlined above. This would ensure an analytically thought process and less use of small scale "gardening" of mangroves as the solution to all mangrove restoration problems. Those involved could then begin to learn more from past successes or failures, act more effectively based on this knowledge, and spend limited mangrove restoration funds in a more cost-effective manner. It will also be important to define criteria for monitoring mangrove restoration projects to include main ecosystem attributes namely: biodiversity, vegetation structure and ecological processes (Ruiz-Jaen and Aide, 2005).

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References

Al-Khayat, J.A., Jones, D.A., 1999. A comparison of the macrofauna of natural and replanted mangroves in Qatar. Est. Coast. Shelf Sci. 49, 55–63.

Adger, W.N., Kelly, P.M., Tri, N.H., 2001. Costs and benefits of mangrove conservation and restoration. In: Turner, R.K., Bateman, I.J., Adger, W.N. (Eds.), Economics of Coastal and Water Resources: Valuing Environmental Functions. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 259–279.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Alongi, D.M., Dixon, P., 2000. Mangrove primary production and belowground biomass in Sawi Bay, Southern Thailand. Phuket Marine Biological Center Special Publication 22, 31–38.

Badola, R., Hussain, S.A., 2005. Valuing ecosystem functions: an empirical study on the storm protection function of Bhitarkanika mangrove ecosystem, India. Environ. Conserv. 32, 85–92.

Barbier, E.B., 2006. Natural barriers to natural disasters: replanting mangroves after the tsunami. Frontiers Ecol. Environ. 4, 124–131.

Berger, U., Rivera-Monroy, V.H., Doyle, T.W., Dahdouh-Guebas, F., Duke, N.C., Fontalvo-Herazo, M.L., Hildenbrandt, H., Koedam, N., Mehlig, U., Piou, C., Twilley, R.R., 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquat. Bot. 89, 260–274.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Kazungu, J., Dehairs, F., Koedam, N., 2005a. Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya. Biol. Conserv. 126, 287–295.

Bosire, J.O., Kairo, J.G., Kazungu, J., Koedam, N., Dahdouh-Guebas, F., 2005b. Predation on propagules regulates regeneration in a high density reforested mangrove plantation. Mar. Ecol. Prog. Ser. 299, 149–155.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Koedam, N., 2003. Colonization of non-planted mangrove species into restored mangrove stands in Gazi Bay, Kenya. Aquat. Bot. 76, 267–279.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Wartel, S., Kazungu, J., Koedam, N., 2006. Success rates of recruited tree species and their contribution to the structural development of reforested mangrove stands. Mar. Ecol. Prog. Ser. 325, 85–91.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Spatial macrobenthic variations in a tropical mangrove Bay. Biodiv. Conserv. 13, 1059–1074.

Brander, L.M., Florax, R.J.G.M., Vermaat, J.E., 2006. The empirics of wetland valuation: a comprehensive summary and a meta-analysis of the literature. Environ. Res. Econ. 33, 223–250.

Brockmeyer Jr., R.E., Rey, J.R., Virnstein, R.W., Gilmore, R.G., Ernest, L., 1997. Rehabilitation of impounded estuarine wetlands by hydrologic reconnection to the Indian River Lagoon, Florida (USA). Wetlands Ecol. Manag. 4, 93–109.

Burns, B.R., Ogden, J., 1985. The demography of the temperate mangrove *Avicennia marina* (Forssk.) Vierh at its southern limit in New Zealand. Aust. J. Ecol. 10, 125–133.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Choudhury, J.K., 1997. Mangroves and other coastal forests Sustainable management of mangroves, forest development and social needs. In: XI World Forestry Congress, vol. 6, Antalya, Turkey, pp. 13–22.

Cole, T.G., Ewel, K.C., Devoe, N.N., 1999. Structure of mangrove trees and forests in Micronesia. For. Ecol. Manag. 117, 90–109.

Cintron-Molero, G., 1992. Restoring mangrove systems. In: Thayer, G.W. (Ed.), Restoring the Nation's Marine Environment. Maryland Seagrant Program, College Park, Maryland, pp. 223–277.

Crona, B.I., Rönnbäck, P., 2005. Use of replanted mangroves as nursery grounds by shrimp communities in Gazi Bay, Kenya. Est. Coast. Shelf Sci. 65, 535–544.

Crona, B.I., Rönnbäck, P., 2007. Community structure and temporal variability of juvenile fish assemblages in natural and replanted mangroves, *Sonneratia alba* Sm., of Gazi Bay, Kenya. Est. Coast. Shelf Sci. 74, 44–52.

Crona, B.I., Rönnbäck, P., Holmgren, S., 2006. Re-establishment of epibiotic communities in reforested mangroves of Gazi Bay, Kenya. Wetlands Ecol. Manag. 14, 527–538.

Dahdouh-Guebas, F., 2001. Mangrove vegetation structure dynamics and regeneration. Ph.D. Sciences Dissertation. Vrije Universiteit Brussel, Brussels, Belgium, 317 pp.

Dahdouh-Guebas, F., Koedam, N., 2002. A synthesis of existent and potential mangrove vegetation structure dynamics from Kenyan Sri Lankan and Mauritanian case-studies. Meded. Zitt. K. Acad. overzeese Wet./Bull. Séanc. Acad. r. Sci. Outre-Mer 48, 487–511.

Dahdouh-Guebas, F., Koedam, N., 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: A review. Aquat. Bot. 89, 80–92.

Dahdouh-Guebas, F., Verheyden, A., De Genst, W., Hettiarachchi, S., Koedam, N., 2000a. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. Bull. Mar. Sci. 67, 741–759.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Koedam, N., 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347, 83–89.

Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Van Speybroeck, D., Koedam, N., 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshwater Res. 49, 345–350.

Dahdouh-Guebas, F., Mathenge, C., Kairo, J.G., Koedam, N., 2000b. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. Econ. Bot. 54, 513–527.

Dahdouh-Guebas, F., Collin, S., Lo Seen, D., Rönnbäck, P., Depommier, D., Ravishankar, T., Koedam, N., 2006. Analysing ethnobotanical and fishery-related importance of mangroves of the East-Godavari Delta (Andhra Pradesh, India) for conservation and management purposes. J. Ethnobiol. Ethnomed. 2, 24.

Devoe, N.N., Cole, T.G., 1998. Growth and yield in mangrove forests of the Federated States of Micronesia. Forest Ecol. Manag. 103, 33–48.

Duke, N.C., Meynecke, J.O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317, 41–42.

Durant, C.L., 1941. The growth of mangrove species in Malaya. Malayan Forester 10, 3–15.

Ellison, A.M., 2000. Mangrove restoration: do we know enough? Restor. Ecol. 8, 219–229.

Ellison, A.M., 2007. Managing mangroves with benthic biodiversity in mind: moving beyond roving banditry. J. Sea Res. 59, 2–15.

Elster, C., 2000. Reasons for reforestation success and failure with three mangrove species in Colombia. Forest Ecol. Manag. 131, 201–214.

Erftemeijer, P.L.A., Lewis, R.R., 1999. Planting mangroves on intertidal mudflats: habitat restoration or habitat conversion? In: Ecotone, VIIIth Seminar, Enhancing Coastal Ecosystem Restoration for the 21st Century, Ranong and Phuket, May 1999, pp. 1–11.

Ewel, K.C., Twilley, R.R., Ong, J.E., 1998. Different kinds of mangrove forests provide different goods and services. Global Ecol. Biogeogr. 7, 83–94.

FAO, 1985. Mangrove Management in Thailand, Malaysia and Indonesia. FAO Environment Paper 4. FAO, Rome.

FAO, 1994. Mangrove Forest Management Guidelines. FAO Forestry Paper 117. FAO, Rome.

Field, C.D., 1996. Restoration of mangrove ecosystems. International Society for Mangrove Ecosystems, Okinawa, Japan, p. 250.

Field, C.D., 1998. Rehabilitation of mangrove ecosystems: an overview. Mar. Poll. Bull. 37, 383–392.

Furukawa, K., Wolanski, E., Mueller, H., 1997. Currents and sediemnt transport in mangrove forests. Est. Coast. Shelf Sci. 44, 301–310.

Gan, B.K., 1995. A Working Plan for the Matang Mangrove Forest Reserve, fourth rev. Published by the State Forest Department of Perak Darul Ridzuan, Malaysia, 214 pp.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: A review. Aquat. Bot. 89, 237–250.

Gong, W.K., Ong, J.E., 1995. The use of demographic-studies in mangrove silviculture. Hydrobiologia 295, 255–261.

Hamilton, L.S., Snedaker, S.C., 1984. Handbook of Mangrove Area Management. East West Centre, Honolulu, Hawaii.

Hogarth, P., 2007. The Biology of Mangroves and Seagrasses Biology of Habitats Series. Oxford University Press, 280 pp.

Hussain, M.Z., 1995. Silviculture of mangroves. Unsylva 46, 36–42.

Kairo, J.G., Dahdouh-Guebas, F., Bosire, J., Koedam, N., 2001. Restoration and management of mangrove systems—a lesson for and from the East African region. S. Afr. J. Bot. 67, 383–389.

Kairo, J.G., Dahdouh-Guebas, F., Gwada, P.O., Ochieng, C., Koedam, N., 2002. Regeneration status of mangrove forests in Mida Creek Kenya: a compromised or secured future? Ambio 31, 562–568.

Kairo, J.G., Lang'at, J.K.S., Dahdouh-Guebas, F., Hansen, L. Bosire, J.O., Karachi, M., 2008. Structural development and productivity of replanted mangrove plantations in Kenya. Forest Ecol. Manag. doi:10.1016/j.foreco.2008.01.031.

Kjerfve, B., 1990. Manual for investigation of hydrological processes in mangrove ecosystems. UNESCO/UNDP Regional Project, Research and its Application to the Management of the Mangroves of Asia and the Pacific (RAS/86/120).

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Kristensen, E., 2007. Mangrove crabs as ecosystem engineers, with emphasis on sediment processes. J. Sea Res. 59, 30–43.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Lee, S.Y., 2007. Mangrove macrobenthos: assemblages, services, and linkages. J. Sea Res. 59, 16–29.

Lewis, R.R., 1992. Coastal habitat restoration as a fishery management tool. In: Stroud, R.H. (Ed.), Stemming the Tide of Coastal Fish Habitat Loss. Proceedings of a Symposium on Conservation of Coastal Fish Habitat, Baltimore, MD, March 7–9, 1991. National Coalition for Marine Conservation, Inc., Savannah, GA, pp. 169–173.

Lewis, R.R., 2000. Ecologically based goal setting in mangrove forest and tidal marsh restoration in Florida. Ecol. Eng. 15, 191–198.

Lewis, R.R., 2005. Ecological engineering for successful management and restoration of mangrove forests. Ecol. Eng. 24, 403–418.

Lewis, R.R., Gilmore Jr., R.G., Crewz, D.W., Odum, W.E., 1985. Mangrove habitat and fishery resources of Florida. In: Seaman, Jr., W. (Ed.), Florida Aquatic Habitat and Fishery Resources. Florida Chapter. American Fisheries Society, Kissimmee, Florida, pp. 281–336.

Lewis, R.R., Marshall, M.J., 1997. Principles of successful restoration of shrimp Aquaculture ponds back to mangrove forests. In: Programa/resumes de Marcuba'97, Palacio de Convenciones de La Habana, Cuba, September 15/20, 1997, p. 126.

Lewis, R.R., Gilmore, R.G., 2007. Important considerations to achieve successful mangrove forest restoration with optimum fish habitat. Bull. Mar. Sci. 3, 823–837.

Macintosh, D.J., Ashton, E.C., Havanon, S., 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. Est. Coast. Shelf Sci. 55, 331–345.

McKee, K.L., Faulkner, P.L., 2000. Restoration of biogeochemical function in mangrove forests. Restor. Ecol. 8, 247–259.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquat. Bot. 89, 155–185.

Ong, J.E., 1982. Mangroves and aquaculture in Malaysia. Ambio 11, 252–257.

Ong, J., Gong, W., Clough, B.F., 1995. Structure and productivity of a 20-year old stand of *Rhizophora apiculata* Blam. mangrove forest. J. Biogeogr. 22, 417–424.

Primavera, J.H., 1997. Fish predation on mangrove-associated penaeids. The role of structures and substrate. J. Exp. Mar. Biol. Ecol. 215, 205–216.

Putz, F., Chan, H.T., 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. Forest Ecol. Manag. 17, 211–230.

Ruitenbeek, J.H., 1994. Modelling economy–ecology linkages in mangroves: economic evidence for promoting conservation in Bintuni Bay, Indonesia. Ecol. Econ. 10, 233–247.

Rönnbäck, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. Ecol. Econ. 29, 235–252.

Rönnbäck, P., Crona, I., Ingwall, L., 2007. The return of ecosystem goods and services in replanted mangrove forests: perspectives from local communities. Environ. Conserv. 4, 313–324.

Rönnbäck, P., Macia, A., Almqvist, G., Schultz, L., 2001. Do penaeid shrimps have a preference for mangrove habitats? Distribution patter analysis on Inhaca Island, Mozambique. Est. Coast. Shelf Sci. 55, 427–436.

Rönnbäck, P., Troell, M., Kautsky, N., Primavera, J.H., 1999. Distribution patterns of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. Est. Coast. Shelf Sci. 48, 223–234.

Ruiz-Jaen, M.C., Aide, T.M., 2005. Restoration success: how is it being measured? Restor. Ecol. 13, 569–577.

Saenger, P., Siddiqi, N.A., 1993. Land from the sea—the mangrove afforestation program of Bangladesh. Ocean Coast. Manag. 20, 23–39.

Saenger, P., 2002. Mangrove Ecology Silviculture and Conservation. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Santilan, N., Hasimoto, T.R., 1999. Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River, New South Wales Australia. Hydrobiologia 413, 95–102.

Sasekumar, A., Chong, V.C., 1998. Faunal diversity in Malaysian mangroves. Global Ecol. Biogeogr. Lett. 7, 57–60.

Sathirathai, S., Barbier, E.B., 2001. Valuing mangrove conservation in southern Thailand. Contemp. Econ. Policy 19, 109–122.

Slim, F.A., Gwada, P.O., Kodjo, M., Hemminga, M.A., 1997. Biomass and litterfall of *Ceriops tagal* and *Rhizophora mucronata* in the mangrove forest of Gazi Bay, Kenya. Mar. Freshwater Res. 47, 999–1007.

Spalding, M., Blasco, F., Field, C., 1997. World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa, Japan, 178 pp.

Srivasatava, P.B.L., Guan, S.L., Muktar, A., 1988. Progress of crop in some Rhizophora stands before first thinning in Matang Mangrove Reserve of Peninsular Malaysia. Pertanika 11, 365–374.

Srivastava, P.B.L., Bal, H.S., 1984. Composition and distribution pattern of natural regeneration after second thinning in Matang mangrove reserve, Perak Malaysia. In: Soepadimo, E., Rao, A.N., Macintosh, D.J. (Eds.), Proceedings of the Asian Symposium on Mangrove Environment: Research Managements, Kuala Lumpar, Malaysia, pp. 761–784.

Stevenson, N.J., Lewis, R.R., Burbridge, P.R., 1999. Disused shrimp ponds and mangrove rehabilitation. In: Streever, W.J. (Ed.), An International Perspective on Wetland Rehabilitation. Kluwer Academic Publishers, The Netherlands, pp. 277–297.

Sukardjo, S., Yamada, I., 1992. Biomass and productivity of a *Rhizophora mucronata* Lamarck plantation in Tritih, Central Java, Indonesia. For. Ecol. Manag. 49, 195–209.

Thampanya, U., Vermaat, J.E., Duarte, C.M., 2003. Colonisation success of common Thai mangrove species as a function of shelter from water movement. Mar. Ecol. Prog. Ser. 237, 111–120.

Triest, L., 2008. Molecular ecology and biogeography of mangrove trees towards conceptual insights on gene flow and barriers: A review. Aquat. Bot. 89, 138–154.

Turner, R.E., Lewis, R.R., 1997. Hydrologic restoration of coastal wetlands. Wetlands Ecol. Manag. 4, 65–72.

Twilley, R.R., 1995. Properties of mangrove ecosystems related to the energy signature of coastal environments. In: Hall, C. (Ed.), Maximum Power. University of Colorado Press, Boulder, Colorado, USA, pp. 43–62.

Vivian-Smith, G., 2001. Box 2.1 Reference data for use in restoring Tijuana Estuary. In: Zedler, J.B. (Ed.), Handbook for Restoring Tidal Wetlands. CRC Press, Boca Raton, Florida, pp. 59–63.

Vogt, K.A., Vogt, D.J., Bloomfield, J., 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests an at ecosystem level. Plant Soil 200, 71–89.

UNDP/UNESCO, 1991. Final Report of the Integrated Multidisciplinary Survey and Research Programme of Ranong Mangrove Ecosystem. RAS/86/120. Bangkok, p. 183.

Walsh, G., Snedaker, S., Teas, H. (Eds.), 1975. Proceedings of the International Symposium on Biology and Management of Mangroves, vols. 1 and 2. Institute of Food and Agricultural Sciences, University of Florida, Florida, p. 846.

Walters, B., 1997. Human ecological questions for tropical restoration: experiences from planting native upland trees and mangroves in the Philippines. Forest Ecol. Manag. 99, 275–290.

Walters, B., 2000. Local mangrove planting in the Philippines: are fisherfolk and fish pond owners effective restorationists? Restor. Ecol. 8, 237–246.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Walton, M.E.M., Samonte-Tan, G., Primavera, J.H., Edwards-Jones, G., Le Vay, L., 2006a. Are mangroves worth replanting? The direct economic benefits of a community-based reforestation project. Environ. Conserv. 33, 335–343.

Walton, M.E.M., Le Vay, L., Lebata, J.H., Binas, J., Primavera, J.H., 2006b. Seasonal abundance, distribution and recruitment of mud crabs (*Scylla* spp) in replanted mangroves. Est. Coast. Shelf Sci. 66, 493–500.

Walton, M.E.M., Le Vay, L., Lebata, J.H., Binas, J., Primavera, J.H., 2007. Assessment of the effectiveness of mangrove rehabilitation using exploited and non-exploited indicator species. Biol. Conserv. 138, 180–188.

Watson, J.G., 1931. The growth of mangrove species. Malayan Forester 1, 217–218.

Wilkie, M.L., Fortuna, S., 2003. Status and trends in mangrove area extent worldwide. Forest Resources Assessment Working Paper 63. Forestry Department, Food and Agriculture Organization of the United Nations, Rome.

Wolanski, E., Mazda, Y., Ridd, P., 1992. Mangrove hydrology. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 43–62.

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Review

Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review

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Abstract

Mangrove ecosystems are considered vulnerable to climate change as coastal development limits the ecosystem services and adaptations important to their survival. Although they appear rather simple in terms of species diversity, their ecology is complex due to interacting geophysical forces of tides, surface runoff, river and groundwater discharge, waves, and constituents of sediment, nutrients and saltwater. These interactions limit developing a comprehensive framework for science-based sustainable management practices. A suite of models have been developed independently by various academic and government institutions worldwide to understand the dynamics of mangrove ecosystems and to provide ecological forecasting capabilities under different management scenarios and natural disturbance regimes. The models have progressed from statistical tables representing growth and yield to more sophisticated models describing various system components and processes. Among these models are three individual-based models (IBMs) (FORMAN, KIWI, and MANGRO). A comparison of models' designs reveal differences in the details of process description, particularly, regarding neighbor competition among trees. Each model has thus its specific range of applications. Whereas FORMAN and KIWI are most suitable to address mangrove forest dynamics of stands, MANGRO focuses on landscape dynamics on larger spatial scale. A comparison of the models and a comparison of the models with empirical knowledge further reveal the general needs for further field and validation studies to advance our ecological understanding and management of mangrove wetlands.

Keywords: Simulation model; Tree growth; Regeneration; Mortality; Hurricane; Sea-level rise; FORMAN; KIWI; MANGRO

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1. Introduction

Mangrove forests grow in coastal settings of (sub)tropical climates characterized by freshwater runoff, multiple substrate conditions, prolonged hydroperiod, salinity, anoxic conditions, and accumulation of toxic substances (Lugo, 1980; Ball, 1996). Species composition is strongly influenced by these coastal settings because they are linked to differences in mangrove tree species' capability to become established and grow. According to Thom (1967), mangroves should be viewed as woody vegetation in the intertidal zone that migrates up and down slope from the sea in relation to eustatic natural and human-induced changes in sea level. In their final remarks, Lugo and Snedaker (1974) conclude that ''mangrove ecosystems are self-maintaining coastal landscape units that are responsive to long-term geomorphological processes and to continuous interactions with contiguous ecosystems in the regional mosaic''. However, when coastal landscapes become fragmented by human transformations of regional and coastal settings, mangroves are less self-maintaining as coastal processes are modified.

Along with coastal processes of geomorphological settings, natural disturbances (e.g., hurricanes) shape the structural complexity of mangrove forests including maximum stand height and tree morphology (Lugo, 1980, 2000; Doyle et al., 1995; Doyle and Girod, 1997; Duke, 2001). The impact of such events may be responsible for multiple equilibrium states that are observed more often than single equilibrium states in mature stands (Lugo, 1997; Duke, 2001). This might be one reason why succession and species composition along hydroperiod and regulator gradients continue to be two of the major research priorities in mangroves (e.g., Lugo and Snedaker, 1974; Ellison et al., 2000; Sherman et al., 2000; Dahdouh-Guebas and Koedam, 2002; Ellison, 2002; Rivera-Monroy et al., 2004; Berger et al., 2006; Castaneda-Moya et al., 2006; Piou et al., in press).

One approach to document forest dynamics employs remote sensing imagery. There are numerous studies that describe temporal changes in spatial extension of mangrove ecosystems (Calzadilla Pérez et al., 2002; Lucas et al., 2002; Cohen and Lara, 2003; Fromard et al., 2004; Hernández-Cornejo et al., 2005; Dahdouh-Guebas and Koedam, 2008) such as shifts in species composition (Dahdouh-Guebas et al., 2000b, 2004, 2005a,b; Kovacs et al., 2001; Wang et al., 2004), changes in mangrove cover before and after natural hazards (Smith et al., 1994; Krauss et al., 2005; Ramachandran et al., 2005), and dynamics of mangrove forest types (Dahdouh-Guebas and Koedam, 2002; Krauss et al., 2005; Simard et al., 2006). Remote sensing approaches document changes in vegetation cover, however they are limited in providing descriptions of ecological processes causing these changes.

Model simulations have been useful in synthesizing current knowledge about mangrove forest dynamics (Doyle and Girod, 1997; Chen and Twilley, 1998; Doyle et al., 2003; Berger and Hildenbrandt, 2000). The modeling approach is suitable for simultaneously evaluating the effects of environmental changes and disturbances on ecological processes such as tree recruitment, establishment, growth, productivity, and mortality. Such estimates on the sustainability of mangrove resources may contribute to evaluating impacts of mangrove degradation to socio-economic systems (Alongi, 2002; Balmford et al., 2002; Macintosh et al., 2002; Rivera-Monroy et al., 2004; Davis et al., 2005). Consequently, simulation models have been proposed as tools for developing management plans for mangrove protection, rehabilitation and restoration (Twilley, 1997; Doyle et al., 2003; Field, 1998, 1999; Duke et al., 2005; Twilley and Rivera-Monroy, 2005). Such utility in resource management requires that model structure captures the mechanisms that explain forest dynamics, such as (a) controlling role of stressors, (b) plant–plant and plant–soil interactions, as well as (c) impacts of natural and anthropogenic disturbances at different temporal and spatial scales (Ellison, 2002; Clarke, 2004).

The first pioneers in mangrove simulation models were Lugo et al. (1976) who used a process-based model to simulate the effects of upland run-off and tidal flushing on the biomass production of an over-washed mangrove wetland. Burns and Ogden (1985) used a Leslie-Matrix model to predict the development of an *Avicennia marina* monoculture assuming an exponential population growth. Clarke (1995) used a Lefkovich matrix for predicting the recovery of an *Avicennia germinans* population following disturbances differing in strength. There are also a few static trophic models estimating matter and energy flow in mangrove ecosystems (e.g. Ray et al., 2000; Vega-Cendejas and Arreguin-Sanchez, 2001; Wolff, 2006). Currently there are only three spatially explicit individual-based simulation models (IBMs) describing Neotropical mangrove forests: FORMAN, KIWI, and MANGRO (Doyle and Girod, 1997; Chen and Twilley, 1998; Doyle et al., 2003; Berger and Hildenbrandt, 2000).

In this paper, we describe these IBMs and discuss their design and specific features. We first explain the essential processes that are assumed to control and regulate mangrove forest dynamics. Based on this assessment, we then compile a list of eight key functional relationships necessary for understanding mangrove forest dynamics. This list will serve as an overview to compare and contrast the purposes and applications of each particular model. Finally, we discuss the application perspectives of IBMs within the field of mangrove ecology, and propose future research directions to continue developing models as research and management tools. The models reviewed focus primarily on the Neotropics, restricting discussion of mangrove forest dynamics to that region.

2. Driving forces of mangrove structure and dynamics

2.1. Linkages between environmental conditions and species performance

According to hierarchy theory (Hölker and Breckling, 2002), processes at a particular organization level can be explained by constraints at higher levels along with mechanisms at lower levels of organization (Pickett et al., 1989). Thus, it is essential to evaluate the climatic and landform characteristics of coastal regions which result in local and often gradual environmental gradients, that represent top-down constrains of mangrove forest development (Fig. 1, Thom, 1984; Woodroffe, 1992; Twilley, 1995; Duke et al., 1998; Twilley et al., 1999b). At the same time, tree performance, growth response, and interactions among trees affect bottom-up patterns of forest development (Smith, 1992).

A conceptual model has been developed that integrates both of these levels of regional environmental constraints and local biotic interactions on the structure and function of mangrove forests (Twilley and Rivera-Monroy, 2005; Fig. 2). According to this model, three types of factors – regulators, resources, and hydroperiod – control mangrove structure and function (Huston, 1994). 'Regulators' are defined as non-resource variables including salinity, sulfide, pH, and redox potential. Resource variables, on the other hand, include nutrients, light or space that are consumed by trees for growth (and thus determine levels of competition). Hydroperiod, the duration, frequency and depth of inundation, is another critical factor controlling mangrove productivity (Wolanski, 1992). According to this model, the interactions among the three factors form a "constraint envelope" which defines the primary productivity of the system. This model links the top-down regional drivers

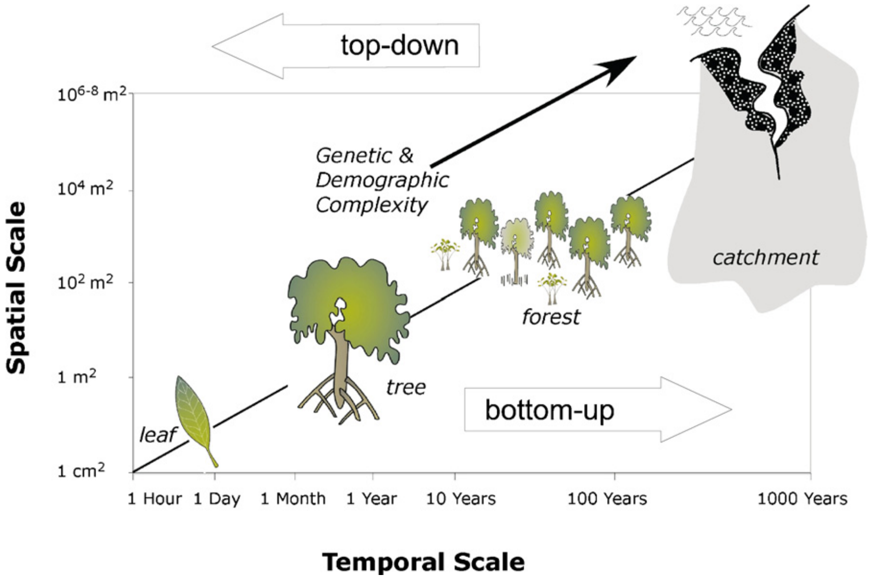

Fig. 1. Temporal and spatial hierarchical organization of key ecosystem components in mangrove forests including leaves, trees, forests and watershed regions. Processes at higher scales include combinations of different species and age classes, with differences in physiology and growth of leaves and trees. These processes affect forest turnover and replacement, depending on landscape scale influences of salinity, elevation, tidal inundation, climate, and geomorphic setting.

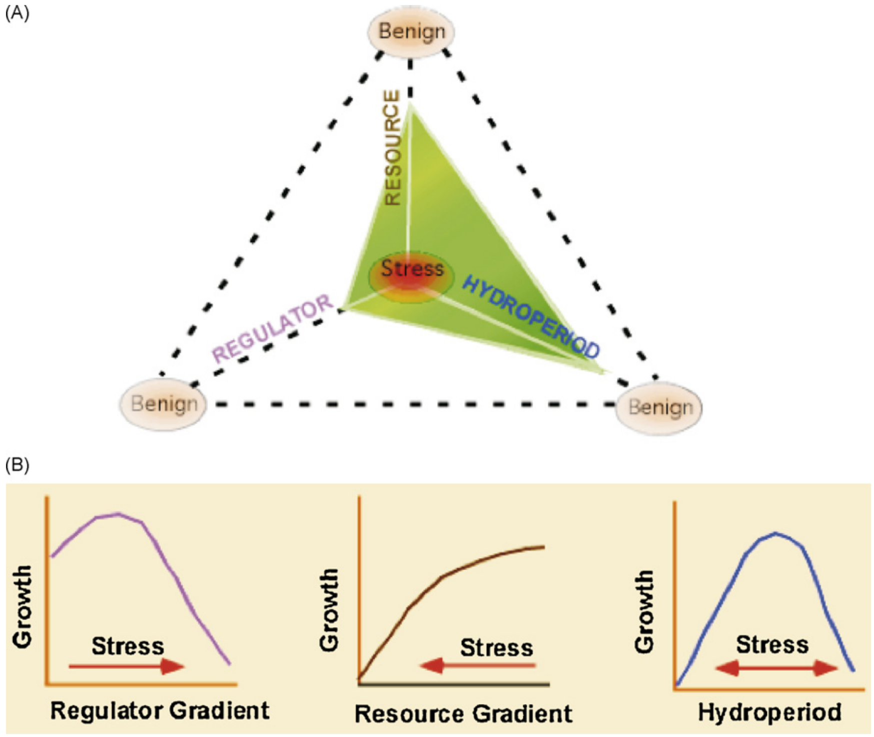

Fig. 2. Factorial interaction of three factors controlling productivity of mangrove forests including regulators, resources, and hydroperiod. (A) Production envelope associated with levels of each factor interaction to demonstrate responding levels of net primary productivity. (B) Definition of stress associated with how gradients in each factor control growth of wetland vegetation (from Twilley and Rivera-Monroy, 2005).

with the bottom-up processes through the responses of individual trees to environmental settings.

In order to analyze a particular forest succession trajectory, it is critical to evaluate ecological processes in more detail. For example, mangrove species adapted to capture photosynthetically active radiation more effectively will have a competitive advantage to colonize available, but shaded, space. In Neotropical mangrove tree species, shade tolerance during seedling and sapling stage decreases from *Rhizophora mangle* and *A. germinans* to *Laguncularia racemosa* (Ball, 1980; Roth, 1992). Yet species-specific irradiance-related tolerances currently have not been evaluated in the field neither in gaps nor under closed canopy.

Nutrients are another key resource that can define growth and spatial distribution patterns in mangrove forests (Kristensen et al., 2008). Neotropical mangrove forests can immobilize nitrogen (N) as a result of high N demand by bacteria decomposing leaf litter (Rivera-Monroy et al., 1995; Rivera-Monroy and Twilley, 1996). This suggests that plant growth might be critically N-limited, depending on the magnitudes of N fixation rates. However, essential nutrients are not necessarily uniformly distributed, and soil fertility can switch from conditions of N- to P-limitation across narrow topographic gradients (Feller and McKee, 1999; Feller et al., 2003a,b). In situ fertilization experiments have shown that nutrient enrichment reduces the efficiency of within-stand and within-tree nutrient conservation mechanisms, which influences species-specific growth rate ratios and, therefore, competition among trees (Lovelock and Feller, 2003).

Salt-tolerance varies among mangrove species (Scholander et al., 1962; Ball, 1998, 2002; Krauss et al., 2008) establishing soil pore water salinity as one of the most critical regulators influencing the structure of mangrove forests (Cintrón et al., 1978; Ball, 1980, 2002; Castaneda-Moya et al., 2006). Studies show that neotropical *R. mangle* and *L. racemosa* have narrower salt-tolerances than *A. germinans* because of their limited ability to balance water and salt uptake. This might be a reason why, *A. germinans* is generally dominant in areas where evaporation exceeds precipitation and soil salinities are $>120\ \mathrm{g\ kg^{-1}}$ (e.g., Cintrón et al., 1978; Castaneda-Moya et al., 2006). Despite numerous reports on species-specific response of propagules to salinity (see e.g., McKee, 1993; Lopez-Hoffman et al., 2007) there is still insufficient knowledge supporting a general mathematical description of this mechanism for propagule establishment up to mature trees along salinity gradients.

Flooded mangrove soils have reducing conditions depending on frequency and duration of standing water and the presence of sulfide. Greenhouse experiments have shown differential tolerance of mangrove seedlings to flooding demonstrating that the interaction between salinity and hydroperiod controls seedling establishment and growth (e.g., Cardona-Olarte et al., 2006). Elevations in mangroves respond to hydroperiod and sediment input, along with feedback effects of mangrove trees that effectively raise the rhizosphere to depths with greater oxygen content. Also, adult trees of *A. germinans* and *R. mangle* are both capable of oxidizing sulfide around the rhizosphere by transporting oxygen through roots (McKee et al., 1988). These mechanisms might explain why adult mangrove plants can grow in soils with high concentrations of sulfide (Matthijs et al., 1999), indicating the large spatial variability of this stressor among and within sites (Rivera-Monroy et al., 2004). Yet, mathematical formulations of how mangroves respond to hydroperiod, particularly mixed with other soil conditions, are poorly understood in mangrove ecology.

Although there are some uncertainties about specific mechanisms linking light, nutrients, salinity, and flooding with tree performance, it is widely recognized that these are essential factors driving mangrove forest dynamics. Thus, simulation models should describe the essential life processes of trees linked to resource, regulator and hydroperiod gradients, and test their relative importance in controlling mangrove forest dynamics (task 1).

2.2. The role of canopy disturbances and gap size on mangrove dynamics

Canopy disturbances at different spatial scales have a strong influence on mangrove forest structure and function, including tree fall, lightning, frost or excessive drought (Lugo, 1980, 2000; Tilman, 1988; Smith, 1992; Smith et al., 1994; Doyle et al., 1995; Fromard et al., 1998; Twilley et al., 1999b; Baldwin et al., 2001; Duke, 2001; Kairo et al., 2002). Specific effects of disturbances depend on their frequency and intensity along resource gradients and hierarchical levels (e.g., hurricanes, deforestation, selective wood cutting) (Gosz, 1992; Roth, 1992; Davis et al., 2005; Ward et al., 2006; Piou et al., 2006; Dahdouh-Guebas et al., 2000a; Glaser, 2003; Walters, 2005; Walters et al., 2008). Although it is desirable to empirically test hypotheses on disturbance regimes, large-scale (>1 km^2) field experiments are often impracticable due to ethical, temporal or spatial constraints. Based on these limitations, there are two further tasks that mangrove models should perform: *test the impact of changes in disturbance regimes on mangrove forest dynamics (task 2), and compile so-called "traffic light lists" which evaluate different management scenarios according to their potential ecological, economic, or social outcome of mangrove sustainability (task 3).*

Disturbances result in resource heterogeneity within a gap, and can be seen as "moving windows of opportunity" for seedling establishment. Several studies document gradients of irradiance and light fleck frequency through gaps; mangrove tree establishment corresponds to these gradients and thus indicates the importance of gaps for forest regeneration (Whelan, 2005; Ward et al., 2006). In contrast, there is little information on changes in nutrient availability or sulfide concentration in such gaps, which possibly could affect re-colonization. Therefore, comparative field studies addressing this topic are needed in addition to simulation experiments *comparing empirical against simulated recovery patterns to test the plausibility of different hypotheses explaining the role of resource gradients in mangrove gaps (task 4).*

The seasonal input of propagules is significant to the recovery rate of a forest from a disturbance, and this recruitment depends on (a) the reproductive phenology of the mature trees, along with the local hydrology (Sherman and Fahey, 2001), and (b) the selective mortality of propagules and seedlings (Lewis, 1982; Cintrón, 1990). Forest recovery also depends on age and size of the individuals that survive disturbances (Shugart, 1984; Botkin, 1993a) such as tree species with re-sprouting capabilities (e.g., *A. germinans* or *L. racemosa*, Baldwin et al., 2001). Survivors will influence light regime, microclimate and soil chemistry and may release propagules immediately within the disturbed area. Therefore, pre-disturbance conditions of previous forest structure and recruitment rates are determinants of mangrove development following a disturbance (Doyle and Girod, 1997; Chen and Twilley, 1998; Berger et al., 2006; Ross et al., 2006; Ward et al., 2006; Piou et al., 2006; Bosire et al., 2008). Thus, mangrove simulation models should: *synthesize the species-specific and age-specific regeneration potential of individual trees after disturbances and their importance for forest recovery (task 5).*

One of the current debates in forest and community ecology is the role of gaps in explaining tree diversity and secondary succession trajectories in temporal, tropical and subtropical forests (Doyle, 1981; Pacala et al., 1993; Denslow et al., 1998; Moorcroft et al., 2001; Felton et al., 2006; Khurana and Singh, 2006; Perry and Enright, 2006). Niche partitioning assumes that competition among individuals for resources determines the diversity of trees regenerating in gaps (Brokaw and Busing, 2000). An opposing view assumes that species composition lacks any specific pattern and is unpredictable, suggesting that no specific successional sequence occurs within gaps following disturbances. Currently, there is not enough information to determine whether niche partitioning or the size of the species pool is more important for the regeneration of canopy gaps in mangrove habitats. Although gap dynamics is recognized as one of the most critical processes regulating mangrove forest structure and productivity, there are only few empirical studies evaluating their impact at different temporal and spatial scales (Sherman et al., 2000; Duke, 2001; Whelan, 2005; Ward et al., 2006). Simulation experiments can focus on dispersal effects and establishment of mangrove trees, and thus contribute *to understanding the roles and relative contribution of interspecific competition and "chance" in structuring mangrove forests following gap formation (task 6).*

Numerous studies in terrestrial forests have shown that the interplay of gap locations, gap frequency, and the successional stage of forest patches at time of gap creation frequently result in a de-synchronization of the successional states of neighboring forest patches and lead to spatial–temporal mosaics of vegetation structure (i.e., the mosaic cycle theory Mueller-Dombois, 1991; Remmert, 1991). Although spatial patterns in mangrove forests have long been recognized, specific gap dynamic studies are lacking in mangrove ecology (but see Dahdouh-Guebas et al., 2000b). One possible explanation is that physical factors like salinity and nutrient cycling have traditionally been considered as sufficiently effective to account for all of the observed structural patterns. To capture the processes associated with gap dynamics, we propose that models should *test the synchronization and de-synchronization effect of canopy disturbances on mosaic cycles of successional* *forest stages on a landscape level to develop a general understanding of mangrove forest dynamics (task 7).*

Now that we have derived these seven key tasks for modeling mangrove, we use these tasks to summarize the specific structure and objectives of published mangrove forest model simulations, as well as their utility in ecological forecasting and natural resources management.

3. From specific data to abstractions: modeling approaches for describing mangrove forest dynamics at different spatial scales

Individual-based models became widely accepted in ecology during the, 1990s and are recognized as suitable tools for simulating the variability of individual plants or animals and its influence on complex life systems (DeAngelis and Gross, 1992; Grimm, 1999; DeAngelis and Mooij, 2005). These models integrate different hierarchical levels of ecological processes, and they can be directly and relatively simply parameterized. They have an intrinsic ability to include both temporal and spatial scales. All these features make them powerful ‘‘virtual laboratories’’, which help testing hypotheses about specific behaviors and traits of individuals, and advance ecological principles for both basic ecological knowledge and the restoration of biological diversity (Urban et al., 1987; Huston et al., 1988; Dunning et al., 1995; Liu and Ashton, 1995; Twilley et al., 1999b). In this section, we describe the three available IBMs focusing on mangrove forest dynamics following the ODD protocol developed to facilitate the comparison and understand model structure and output (ODD = Overview, Design concepts, Detail as described in Grimm et al., 2005, 2006; Grimm and Railsback, 2005).

3.1. Purposes of the models

All three models, FORMAN, KIWI, and MANGRO were developed to understand long-term dynamics of mangrove forests under different environmental and management settings. They are parameterized for the neotropical mangrove species, *R. mangle*, *A. germinans*, and *L. racemosa* (Doyle and Girod, 1997; Chen and Twilley, 1998; Doyle, 1998; Doyle et al., 2003; Berger and Hildenbrandt, 2000), although model applications focus on different (sub)tropical regions. For example, FORMAN was applied to various forests in different coastal locations in Florida (Chen and Twilley, 1998) and Colombia (Twilley et al., 1999b). The KIWI model was applied to mangrove forests in North Brazil (e.g., Berger et al., 2006) and Belize (Piou et al., in press; Piou, 2007). Only recently, this model was parameterized for *Rhizophora apiculata*, a mangrove species occurring in the Indo-West-Pacific region (Fontalvo et al., in preparation). Embedded in the landscape scale vegetation model SELVA, the MANGRO model has the most specific regional focus: the Everglades in south Florida, USA. The specific purposes of each model application also differ ranging from the assessment of management scenarios, forecast of landscape development, and assessment of theoretical ecological issues (see Table 1).

3.2. State variables and spatial scales

All three models describe a tree by its species and stem diameter, which are used to derive other descriptors such as stem height and biomass. The models differ in the spatial description of the trees including stem position, leaf area, and crown dimension (see also Table 1). The FORMAN model is a

Table 1
Differences of the FORMAN, KIWI, and MANGRO models in structure and design

	FORMAN	KIWI	MANGRO
Differences in purpose(s)	Applied to particular sites in Florida, Louisiana, and Colombia	Applied to theoretical issues, and particular sites in Brazil and Belize	Applied to the Everglades (Florida, USA)
Differences in variables	No explicit stem position, leaf area	Stem position, size and shape of FON, no leaf area	Stem position, crown dimension, leaf area
Differences in spatial scales	Forest stand (matrix of gaps 500 m^2 each)	Forest stand with variable extension and shape	Landscape as matrix of squared forest stands (default size 1 ha)
Differences in resource description	Nutrients/salinity homogeneous within a gap. Light availability per height class	Nutrients/salinity heterogeneous. Light availability implicitly	Salinity/soil quality homogeneous within stand. Light availability per tree
Differences in design concepts	*Interactions of trees*: light competition through sum of leaf areas per height class. *Sensing of trees*: nutrients/salinity within gap, neighbors via total leaf area above, number of degree days	*Interactions of trees*: competition for all spatial distributed resources phenol-menologically via FON. *Sensing of trees*: nutrient/salinity at stem position, neighbors in spatially explicit constellation, no temperature sensing	*Interactions of trees*: competition for growing space and light explicitly. *Sensing of trees*: flooding/salinity/stand quality at stand unit, neighbors via distance and azimuth
Differences in initialization	Saplings	Saplings	Seedlings
Differences in submodels	No explicit saplings dispersal. *Tree growth* affected by nutrients, light, and temperature defined growth period. *Tree mortality* due to age and growth suppression, gap creation by a reduction of total leaf area	Explicit saplings dispersal. *Tree growth* affected by nutrients, neighbor competition (FON overlap). *Tree mortality* due growth suppression, gap creation spatially explicit	No explicit seedlings dispersal. *Tree growth* affected by flooding, crown volume, light. *Tree mortality*: due to growth suppression, gap creation spatially explicit

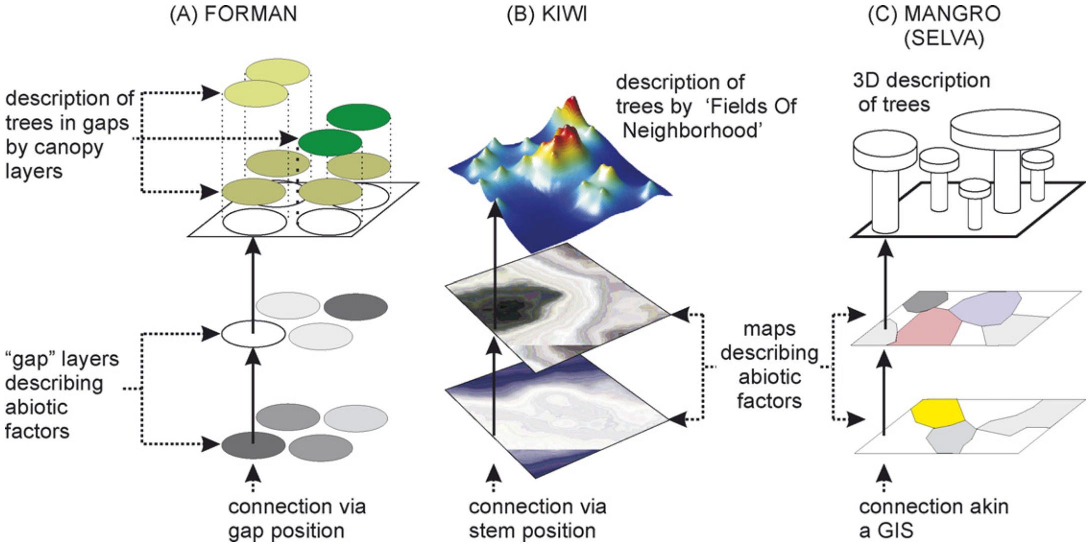

Fig. 3. Vertical and horizontal considerations of the mangrove models. Individual subfigures represent (A) the FORMAN model describing vertical competition for light in even sized gaps. Different layers describe abiotic factors like salinity or nutrient availability. They are connected by the gap position. The factors may vary among but not within the gaps. (B) The KIWI model represents individual trees by ''fields-of-neighborhood'' describing the intensity of competition exerted by the trees against their neighbors. Map layers representing abiotic factors are connected by the stem positions of the trees. (C) The MANGRO model represents each tree in its 3D architecture including spatial position, stem diameter, stem height, crown dimension, and leaf area. All data layers are connected akin to a Geographical Information System.

gap model with a code based on the JABOWA and FORET models (Botkin et al., 1972; Shugart, 1984, see also Fig. 3A). The forest stand is assumed as a composite of many gaps, which do not interact with each other. The gaps described in FORMAN are equal-sized (500 m^2) corresponding to the area covered by single large, dominant trees in natural forests. The specific location of a tree within a gap is not considered in FORMAN, and light competition is represented by stratified, averaged leaf layers. Also salinity and nutrient availability are assumed to be homogeneous within a gap. The authors generated other models to simulate these parameters (e.g. NUMAN and HYMAN models), yet those models are not directly linked with the simulation of the FORMAN model (Chen and Twilley, 1999; Twilley et al., 1999a).

The KIWI model characterizes each tree by its stem position within a Cartesian coordinate system. Tree competition is spatially explicit: each tree has a size-dependent circular zone around its stem. The overlap of these circular zones defines the competition among neighbor trees (Fig. 3B). In contrast to 'zone-of-influence' (ZOI) models, KIWI superimposes a scalar field on the ZOI. This field, or FON ('field-of-neighborhood'), decreases from the stem to its boundary and represents declining competition strength with increasing distance from the stem. This approach thus links the ZOI approach with so-called Ecological Field (EF) theory (see Berger and Hildenbrandt, 2000; Berger et al., 2002 for further details). The extension and shape of the forest stand are chosen by the experimenter and may thus correspond directly to natural stand conditions. Typical experiments have used stand sizes from 100 to 10,000 m^2. The physical environment like topography, inundation height, inundation frequency, salinity and nutrient availability are mapped explicitly by user-supplied layers corresponding to the simulated stand coordinate system (Fig. 3B).

The MANGRO model represents trees in its three-dimensional architecture (Fig. 3C). Trees are simulated in square plots of side dimensions of no less than dominant tree height or larger. A stand is a composite of many plots; the default stand size is 1 ha. Each tree and stand is spatially defined by latitude and longitude. MANGRO has the flexibility to run as a stand-alone stand simulator like FORMAN and KIWI with user-specified inputs, or in a hierarchically linked mode with the SELVA model which manages landscape level forcing functions and site conditions, such as mean monthly sea level, soil elevation, daily river flow, hurricane recurrence, predicted wind speed and potential for lightning strike. SELVA can also provide disturbance probabilities from the larger landscape unit, which may be user-specified at the regional, continental, or global scale.

3.3. Processes overview and scheduling

All three models use discrete time steps of one simulation year. Within each year the following processes occur: establishment of seedlings/saplings, growth of existing trees, and tree mortality. The stem diameter of all trees is updated synchronously. From this update, the specific derived parameters such as tree height are also re-calculated.

3.4. Design concepts

3.4.1. Emergence

In all three models, population dynamics (e.g., the temporal variation of basal area, a specific vertical height structure, or species dominance) emerges from the life processes (establishment, growth and mortality) of trees modified by competition and abiotic conditions. Due to the explicit description of trees local constellations, the following characteristic patterns emerge in forests simulated by the KIWI model: clumped to regular spatial distribution of trees, spatial grouping of species, size-class- or fitness-dependent frequency distributions of trees. During MANGRO simulations within the frame of the SELVA-model, landscape change emerges as a process of collective stand responses and habitat redistribution by migration or retreat.

3.4.2. Interaction

In FORMAN, trees interact through vertical competition for light described by the sums of leaf areas as proxies for the transparencies of height classes. This competition for light is dependent on growth potential of each species to nutrient and salinity conditions explicitly described for the plot. In KIWI, trees compete via their field-of-neighborhood for all spatially distributed resources, which are not specified explicitly. In MANGRO, trees compete for growing space and light within and between canopy layers, horizontally and vertically considering the position and shading of neighboring trees, thereby affecting crown geometry, light attenuation, and reception.

3.4.3. Sensing

Tree growth is influenced by the salinity and nutrient availability in the gap (FORMAN), at stem position (KIWI), or at each tree and stand unit (MANGRO model). In FORMAN, trees are "informed" about the presence of neighboring trees by the total leaf area in the canopy above them. In KIWI, the influence of neighbors on a tree is described by overlapping FONs considering the distance, explicit location and size of all neighbors. In MANGRO, neighbor competition is described in terms of the distance among the trees and the azimuth of every neighbor tree. In FORMAN applications to Florida, trees growth is influenced by the species-specific extension of the annual growth period, defined by an annual accrued number of degree days above some threshold temperature. This feature is not implemented in the KIWI model which was exclusively applied to tropical forests without temperature growth limitation so far.

3.4.4. Stochasticity

During the initialization, trees are randomly distributed over the gaps (FORMAN) or within the stand (KIWI, MANGRO) when eligible and unoccupied space is available. Tree mortality by disturbances is also described as a random function.

3.4.5. Observation

All three models provide a yearly tracking of variables on individuals such as stem diameter and stem height, and on stand level such as total basal area, importance values, or complexity indices.

3.5. Initialization

All three models provide variations in initial data depending on selected scenario or data availability. While smallest trees (assumed to be saplings) have a minimum height of 1.27 m in the FORMAN and KIWI model, MANGRO also describes first year seedlings. The initial number of trees and the species composition can be set corresponding to the requirements of the particular experiment. However, 30 individuals per species per 500 m^2 are used on average in the FORMAN model. For the KIWI model, a typical initial density is 300 individuals per species per 10,000 m^2. The default mode of the MANGRO model allows full stand stocking for every square meter of unoccupied space.

3.6. Input

The models use sapling (FORMAN, KIWI) or seedling (MANGRO) recruitment rates per species defining quasi-externally the annual establishment of new trees. Furthermore, abiotic conditions (e.g., salinity, nutrient availability or stand quality, which are parameters characterizing the inundation regime) are given for each gap (FORMAN), tree location (KIWI) or stand (MANGRO) and may be temporally variable. Discrete events modulating tree mortality (natural hazards, tree cut) or an overall disturbance regime can be scheduled at each time step as required by the experiment.

3.7. Submodels

3.7.1. Recruitment and establishment

In FORMAN and KIWI, seedling growth is not explicitly simulated for two reasons: (a) due to lack of field data, and (b) in order to save computational expense. However, factors affecting seedling growth and mortality – such as grazing or sulfides – are implicitly included in sapling recruitment rates. In FORMAN, the annual number of established saplings added to a gap is arbitrary based on empirical evidence of biotic and abiotic factors controlling recruitment. Following establishment, growth is controlled by available light and soil conditions (nutrients and salinity). In KIWI, the potential location of a sapling is chosen randomly, including a range restriction to simulate establishment beneath a parent tree. Yet, trees can only establish if competition of existing trees is below a given species-specific threshold simulating shade-tolerance of the sapling. In the MANGRO model, stands are stocked with new recruits for every square meter of unoccupied space released by the eventual death of standing trees. In addition, the MANGRO model possesses several seedling regeneration submodels that control species recruitment relative to site elevation, tidal flooding, and proximity and composition of neighboring mangrove stands. In all three submodels, the local recruitment rate of each species can be a function of parent tree density and establishment might be modified by environmental conditions such as salinity, sea level, soil elevation, and flooding potential expressed as gap characteristic or depending on tree location in the flooding gradient.

3.7.2. Tree growth

All three models use the JABOWA-type growth function and a yearly time step. Stem increment is a function of stem diameter in breast height (dbh), tree height, and the maximum values of dbh and height for a given tree species. This function and its parameterization are defined for optimal growth conditions. To simulate sub-optimal conditions and stress, growth multiplier functions correct the stem increment depending on salinity conditions and available nutrients (total soil P). The FORMAN model also uses correction functions for the light availability and temperature-defined length of the annual growth period. In the KIWI model, a multiplier function considering a neighbor effect is introduced. The intensity of a neighbor's field-of-neighborhood (FON) exerted on the FON of the focal tree is taken as measure for this multiplier. Unlike FORMAN and KIWI, MANGRO contains no nutrient functions, but models site fertility implicitly as a function of maximum potential tree height. Annual stem diameter increase depends on species growth potential for a given tree diameter reduced by derived crown volume, light availability, and light quality. Flooding and salinity further modify stem growth. Crowns grow as a function of crown space and pre-eminence as to which tree fills space first for a given crown height and class. Crown structure is modeled as a three-dimensional process of crown height, width, and depth in relation to sun angle and shading by neighboring trees.

3.7.3. Mortality

All current individual-based mangrove models describe sapling mortality explicitly. The FORMAN and the KIWI model consider the factors that limit seedling establishment (predation, stress, hydroperiod) by sapling recruitment rates. For trees, there is a similar source of mortality in all three models: the probability of tree mortality risk increases after a prolonged period of growth suppression resulting from the compound effect of salinity stress, nutrient limitation, and/or neighborhood competition. In the FORMAN model, mortality is triggered if the annual stem increment is below a specified threshold in two subsequent years. In the KIWI model, a tree dies if the mean stem increment over a user-supplied time range (typically 5 years) is less than half of the average increment under optimal conditions. Such a growth suppression is more frequently met when the environmental conditions constantly deteriorate and when a tree stem diameter approaches the species-specific maximum. Whereas KIWI uses these conditions for an indirect description of tree mortality depending on tree age, an explicit function is used in the FORMAN model. Here, a tree dies with a certain probability which increases with age (as in Botkin, 1993b). However, by considering growth suppression within a time window of several years, a tree has a chance to 'convalesce' when conditions after a shorter stress period ameliorate, that is, salinity decreases, more nutrients become available, or when a neighbor trees die. Also, all three models consider tree death due to stochastic events. In FORMAN and KIWI probabilities (e.g., that a hurricane appears in a particular year and affects a certain percentage of trees) are controlled by the experimenter. For the MANGRO model, the separate HURASIM model reconstructs wind fields from historic storm data for each land unit managed by SELVA and relates specific storm data to each distributed MANGRO model which describes species-specific tree mortality functions for given wind speeds (Doyle and Girod, 1997). Mortality due to cutting of trees or lightning strikes can be implemented similarly in the three models. This might lead to a decrease of leaf area in the particular height class of a gap (FORMAN model), to the creation of circular gaps according to a gap size distribution (MANGRO model), or to canopy gaps of various sizes and shapes (KIWI model).

3.7.4. Evaluation

The robustness of all three models has been tested by classical sensitivity analyses (Doyle and Girod, 1997; Chen and Twilley, 1998; Piou, 2007). For testing the suitability of the models for simulating particular mangrove stands, model results have been regularly tested against field patterns. Total basal area simulated for the Shark river estuary by the FORMAN model was within ±10% of that observed in the field (Chen and Twilley, 1998). Doyle and Girod (1997) shows similar results regarding forest structure of south Florida mangrove ecosystems. Berger et al. (2004) demonstrates that the KIWI model produces both mixed size classes (with a size class dominance in less disturbed stands), and a u-shaped stem diameter size class distribution of the dead trees corresponding to empirical time series (Monserud and Sterba, 1999) and other modeling studies (Keane et al., 2001). Piou (2007) developed an information criterion based on the Akaike's Information Criterion, the so-called Pattern-Oriented-Information-Criterion (POMIC). This technique was applied to evaluate how well different KIWI parameterizations reproduce zonation patterns of Belizean mangroves by "visual debugging" methods (Piou, 2007). The latter method was also applied to the vertical canopy structure during secondary succession (Berger et al., 2006) to tune the KIWI model for a mangrove forest in North Brazil.

3.7.5. Availability

The KIWI model is available on demand via the corresponding author. The online appendix of this paper gives an overview about model's output.

4. Contribution of individual-based modeling to understanding mangrove forest dynamics: advances and challenges

Given the generality, objectives and applications of the FORMAN, KIWI, and MANGRO models, they have contributed to the synthesis of available quantitative and qualitative knowledge of mangrove forests. All three models describe the essential life processes of trees (establishment, growth, and mortality) depending on resources (light, nutrients), regulators (salinity), and competition (task 1). Model simulations demonstrate how environmental constraints in a given geomorphological setting influence forest dynamics. For example, using FORMAN simulation experiments, Chen and Twilley (1998) showed that resource competition for nutrient availability from marine to mesohaline environments might explain a reduction in *A. germinans* and *L. racemosa* basal areas as observed in the Shark river estuary following impacts by

Hurricane Donna in 1960. The same study illustrated that the relative rates of recruitment of *A. germinans*, *L. racemosa,* and *R. mangle* over time was also significant to explain spatial patterns in forest dynamics. Simulation experiments with KIWI showed that a temporal decrease in nutrient availability in combination with species-specific differences in nutrient-uptake efficiency between *L. racemosa* and *A. germinans* (Lovelock and Feller, 2003) were likely to explain the gradual replacement of the pioneer species (*L. racemosa*) in the canopy as observed on northern Brazil after the abandonment of rice cultivation fields (Berger et al., 2006). These findings compare with studies in tropical wet forests where gaps with high nutrient pools significantly affected more the growth rates of high-light demanding species than those of shade-tolerant species.

In addition to demonstrating the role of nutrient concentrations in forest growth, simulation experiments also indicate the significant effects of tree-to-tree competition on forest structure. For example, KIWI simulations support the hypothesis that the slope of the so-called self-thinning-line is not fixed but confined in two directions, i.e., the strength of neighbor competition defines the upper limit whereas morphological constraints such as the stem diameter versus crown diameter relationship determines the lower limit (Berger et al., 2002, 2006). Furthermore it appears that the self-thinning line is linked to a homogenization process in the plot forcing the symmetry of the stem diameter distribution (Berger and Hildenbrandt, 2003). In general, KIWI applications frequently address theoretical issues in vegetation ecology such as asymmetric competition among plants, or the age-related declines in forest production (e.g., Bauer et al., 2004; Berger et al., 2004).

All three mangrove models have been used to test the impact of natural and human-induced disturbances on forest dynamics (task 2). Twilley et al. (1999b) used the FORMAN model to simulate the impact of different restoration regimes on the recovery of mangroves in the Ciénaga Grande de Santa Marta, Colombia (CGSM) in specific site conditions and at decadal time scales. The authors predicted forest recovery in terms of basal area and species composition depending on different scenarios of freshwater inflow, natural recruitment, and planting regimes. Berger et al. (2006) simulated the secondary succession of mangroves after clear-cutting and rice cultivation under brackish water conditions in the Bragança peninsula, North Brazil. Simulations suggested that a combination of disturbance history, nutrient and/or salinity heterogeneity determines species growth potential, but biogenic changes in abiotic conditions, tree competition, and dispersal actually defines the succession trajectory. This study showed that these factors could create multiple outcomes in terms of species composition, even in forests with only a few species under optimal growth conditions. Doyle and Girod (1997) applied hindcast simulations of the MANGRO model linked with a hurricane simulation model, HURASIM, to evaluate the effect of hurricane history on the landscape composition and structure of mangroves in the Florida Everglades. They identified the occurrence of major storms every 30 years as the most important factor controlling mangrove structure and dynamics in south Florida. Based on forecast simulations with more intense storm events expected under projected climate change, the authors predicted a further alteration in the landscape structure and composition during the next century.

In principle, all revised IBMs provide a framework for evaluating management scenarios according to their potential ecological, economic, or social outcome of mangrove sustainability (task 3). MANGRO simulations of future sea-level rise from climate change suggest that tidal inundation increases across the Everglades landscape and enhances mangrove encroachment and expansion onto the low-lying Everglades slope (Doyle et al., 2003). The MANGRO model also considers management options such as hydrologic restoration of freshwater flow in the Everglades which may help to stall the rate of mangrove expansion into former freshwater habitats under rising sea levels and future climate change. Twilley et al. (1999b) used FORMAN to evaluate potential management scenarios regarding the hydrological regime, which was proposed for the rehabilitation of CGSM. The authors compile a so-called ‘‘traffic light list’’ signifying which scenario is best (‘‘green light’’), intermediate (‘‘yellow light’’), or worst (‘‘red light’’) in terms of basal area recovery and species composition.

A comparison of empirical versus simulated recovery patterns is a suitable strategy to test the plausibility of different hypotheses regarding resource gradients in gaps (task 4). This procedure refers to the strategy of ‘‘Pattern-Oriented-Modeling’’ (Grimm and Railsback, 2005) and is a general advantage of spatially explicit, individual-based models. Berger et al. (2006) use a comparison of temporal changes in canopy structure (height differentiation and species composition) to explain recovery phenomena of mangrove forests. Similarly, Doyle and Girod (1997) compared forest structure of field plots with simulated results to gauge the contribution and role of hurricanes in controlling forest dynamics of south Florida mangrove ecosystems. Finally, Piou (2007) tested the importance of intertidal gradients for the establishment and growth processes of Caribbean mangroves in an attempt to reproduce the recovery of Belizean sites destroyed by hurricane Hattie in 1961.

5. Recommendations, future research directions, and conclusions

Despite the successful model applications described above, there still exist several model limitations and underutilized model resources that restrict the use of these tools to advance our understanding of mangrove forest dynamics. For example, all three mangrove forest simulators have been used to evaluate the relative role of niche partitioning and ‘‘chance’’ in structuring mangrove forests (task 6), but to a different extent according to their formulation of the recruitment process. Comparing the simulation results of the three different mangrove IBMs under similar scenario and disturbance regimes could evaluate the relative importance of recruitment and specific sapling dispersal mechanisms on regulating forest trajectories over time which have been suggested by empirical studies (e.g. Thampanya et al., 2002; Thampanya, 2006). Nevertheless, specific factors determining seedling and sapling survival rates such as predation are not explicitly formulated in model simulations. There is only one IBM, the so-called IBU model, which simulates local movement of individual *Ucides cordatus* crabs (Piou et al., 2007). This model has been used to analyze recovery patterns of a crab population after fishing in North Brazil. A link of such a model to forest dynamics through microhabitat conditions, leaf litter consumption and seed predation is still an open research question (cf. Cannicci et al., 2008).

There is no consensus about the detail of physiological mechanisms and competition processes needed for more accurate modeling of forest dynamics (Busing and Mailly, 2004). Regarding mangrove forests, this question is particularly critical since physiological field studies in mature forests are lacking in comparison to mesocosms and greenhouse studies (e.g., Cardona-Olarte et al., 2006). Further studies comparing simulations of FORMAN, KIWI, and MANGRO models to determine whether more detailed formulations of the spatial distribution of resources like light and tree dimensions such as crown volume and orientation can significantly improve model accuracy as suggested by Reynolds and Ford (2005).

Field studies on vegetation patch dynamics show that gap size influences forest dynamics (e.g., Pickett and White, 1985). For example, pioneer species are often excluded when gap size falls below a certain level; these small gaps might restrict regrowth and promote closure from the surrounding canopy (Baldwin et al., 2001). KIWI and MANGRO address this aspect because gaps of different sizes and shapes appear ‘‘naturally’’ when trees die. In this case, the created gap conditions control dispersal, establishment, survivorship, and growth of new recruits. However, to enhance our understanding of the relative importance of resource gradient partitioning and recruitment limitation in maintaining tree species richness and spatial distribution, further simulation experiments are needed. Such experiments should be linked to integrative (across scales) field experiments on the relationship among gap and patch geometry and on species distribution in mangrove forests. Moreover, there is a need for both comparative and multifactor experiments designed to examine how soil nutrient concentrations and hydroperiod interact with stressors to limit growth of both seedlings and adult trees (e.g., Thampanya et al., 2002; Cardona-Olarte et al., 2006). In this context, mechanistic submodels could be suitable to support the analysis of field experiments which are often hard to interpret with increasing complexity.

FORMAN and MANGRO have focused on site-specific predictions of forest productivity, and although SELVA–MANGRO (Doyle and Girod, 1997; Doyle et al., 2003) and FORMAN (Twilley et al., 1999b) have also simulated regional productivities and responses to global change, model results are limited due to the lack of a description of belowground processes (Twilley et al., 1992). This limitation includes multilayer representation of soil water and nutrient availability as well as processes like biomass allocation to roots and root distribution within the soil, which have been neglected in mangrove research (but see Komiyama et al., 1987, 2008). Currently, there is only one published mangrove nutrient mechanistic model that simulates profiles of soil carbon, N and P and organic matter (NUMAN; Chen and Twilley, 1998). We also describe the need to produce a synthesis of the species-specific and age-specific regeneration potential of individual trees after disturbances and their importance for system recovery as grasped by the simulation models (task 5). The MANGRO model partly focuses on this topic by including an adaptive function for effecting tree growth rate and performance based on disturbance (Doyle and Girod, 1997). Nevertheless, investigations regarding the importance of re-sprouting on the recovery of mangrove systems after mechanical disturbances cannot be carried out by the available IBMs. Current models do not provide the needed flexibility in representation of tree architecture (e.g., sprouting branches and deviations from circular crown shapes), which could be an important process for analyzing system recovery after mechanic disturbances, like hurricanes. Until now, the ‘‘virtual trees’’ do not show ‘‘adaptive behavior’’. Trees grow faster or slower based on environmental conditions and their local neighborhood, but they are unable to respond in terms of reproduction time, reproduction type, or specific tree morphology (e.g., asymmetry of tree extension, scrub stature, or tree shape). The lack of phenotypic plasticity is a general limitation of plant models (Grimm and Railsback, 2005).

Since all three models describe landscape vegetation patterns, they are suitable to test the synchronization and desynchronization effect of canopy disturbances on mosaic cycles of successional forest stages on a landscape level (task 7). This is, however, an open challenge and still on the list of potential applications of the FORMAN, KIWI, and MANGRO models.

We further suggest to replicate field and mesocosm experiments across latitudinal gradients (see, e.g., Cardona-Olarte et al., 2006), or within a wider geographic range, to determine the relative importance of interacting factors such as climatic settings or specific adaptations of spatially distant populations, on forest dynamics. In this context it is necessary to stress that parameterization of the current mangrove IBMs is based on data collected within a very narrow geographical range. Stem growth data as well as information about tree age and mortality from different regions of the world are essential to test the general applicability of current simulation experiment results (see, e.g., Menezes et al., 2003; Verheyden et al., 2005). Model applications to mangrove forests in Africa, Asia, or Australia could support research related to coastal protection and sustainable use of coastal wetlands worldwide, but will depend on the acceptance of such models as research tools for developing management recommendations.

The mangrove models discussed in this paper have contributed to the understanding of critical processes in mangrove wetlands by identifying relationships and mechanisms that need further study; particularly those regulating recruitment, productivity and forest structure. Being complex hypothesis formulations, our models are part of the scientific method, and serve as ‘‘blue prints’’ to define research priorities (Wullschleger et al., 2001). This paper uniquely summarizes the advances and applications of existing forest simulation models that have been independently designed to understand mangrove forest dynamics and management. Hopefully, this review will spur additional field and modeling research that will enhance and expand model functionality and utility for a better understanding of one of the most productive ecosystems in the world.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.aquabot.2007.12.015.

References

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.

Baldwin, A.H., Egnotovich, M.A.F., Platt, W.J., 2001. Regeneration in fringe mangrove forests damaged by Hurricane Andrew. Plant Ecol. 157, 151–164.

Ball, M.C., 1980. Patterns of secondary succession in a mangrove forest of southern Florida. Oecologia 44, 226–235.

Ball, M.C., 1996. Comparative ecophysiology of mangrove forest and tropical lowland moist rainforest. In: Tropical Forest Plant Ecophysiology, Chapman & Hall, New York, pp. 461–496.

Ball, M.C., 1998. Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River floodplain, northern Australia. Global Ecol. Biogeogr. Lett. 7, 73–82.

Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. Trends Ecol. Evol. 16, 126–139.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K., Turner, R.K., 2002. Economic reasons for conserving wild nature. Science 297, 950–953.

Bauer, S., Wyszomirski, T., Berger, U., Hildenbrandt, H., Grimm, V., 2004. Asymmetric competition as natural outcome of neighbour interactions among plants: results from the field-of-neighbourhood modelling approach. Plant Ecol. 170, 135–145.

Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecol. Model. 132, 287–302.

Berger, U., Hildenbrandt, H., Grimm, V., 2002. Towards a standard for the individual-based modeling of plant populations: self-thinning and the field-of-neighborhood approach. Nat. Resour. Model. 15, 39–54.

Berger, U., Hildenbrandt, H., 2003. The strength of competition among individual trees and the biomass-density trajectories of the cohort. Plant Ecol. 167, 89–96.

Berger, U., Hildenbrandt, H., Grimm, V., 2004. Age-related decline in forest production: modelling the effects of growth limitation, neighbourhood competition and self-thinning. J. Ecol. 92, 846–853.

Berger, U., Adams, M., Grimm, V., Hildenbrandt, H., 2006. Modeling secondary succession of neotropical mangroves: causes and consequences of growth reduction in pioneer species. Perspect. Plant Ecol. Evol. Syst. 7, 243–252.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: A review. Aquat. Bot. 89, 251–259.

Botkin, D.B., 1993a. Forest Dynamics. Oxford University Press, Oxford, New York.

Botkin, D.B., 1993b. Forest Dynamics—An Ecological Model. Oxford University Press, New York.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.

Brokaw, N., Busing, R.T., 2000. Niche versus chance and tree diversity in forest gaps. Trends Ecol. Evol. 15, 183–188.

Burns, B.R., Ogden, J., 1985. The demographic of the temperate mangrove (*Avicennia marina* (Forsk. Vierh.) at its southern limit in New Zealand. Aust. J. Ecol. 10, 125–133.

Busing, R.T., Mailly, D., 2004. Advances in spatial, individual-based modelling of forest dynamics. J. Veg. Sci. 15, 831–842.

Calzadilla Pérez, A., Damen, M.C.J., Geneletti, D., Hobma, T.W., 2002. Monitoring a recent delta formation in a tropical coastal wetland using remote sensing and GIS. Case study: Laguna de Tacarigua, Venezuela. Environ. Dev. Sustain. 4, 201–219.

Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunistic impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89, 186–200.

Cardona-Olarte, P., Twilley, R.R., Krauss, K.W., Rivera-Monroy, V., 2006. Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. Hydrobiologia 569, 325–341.

Castaneda-Moya, E., Rivera-Monroy, V.H., Twilley, R.R., 2006. Mangrove zonation in the dry life zone of the Gulf of Fonseca, Honduras. Estuar. Coasts 29, 751–764.

Chen, R., Twilley, R.R., 1998. A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. J. Ecol. 86, 37–51.

Chen, R., Twilley, R.R., 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River estuary, Florida. Estuaries 22, 955–970.

Cintrón, G., 1990. Restoration of Mangrove Systems. National Oceanic and Atmospheric Administration, Washington, DC.

Cintrón, G., Lugo, A.E., Pool, D.J., Morris, G., 1978. Mangrove in arid environments in Puerto Rico and adjacent Islands. Biotropica 10, 110–121.

Clarke, P.J., 1995. The population dynamics of the mangrove *Avicennia marina*; demographic synthesis and predictive modelling. Hydrobiologia 295, 83–88.

Clarke, P.J., 2004. Effects of experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. J. Ecol. 92, 2003–2213.

Cohen, M.C.L., Lara, R.J., 2003. Temporal changes of mangrove vegetation boundaries in Amazonia: application of GIS and remote sensing techniques. Wetlands Ecol. Manage. 11, 223–231.

Dahdouh-Guebas, F., Mathenge, C., Kairo, J.G., Koedam, N., 2000a. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. Econ. Bot. 54, 513–527.

Dahdouh-Guebas, F., Verheyden, A., De Genst, W., Hettiarachchi, S., Koedam, N., 2000b. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. Bull. Mar. Sci. 67, 741–759.

Dahdouh-Guebas, F., Koedam, N., 2002. A synthesis of existent and potential mangrove vegetation structure dynamics from Kenyan, Sri Lankan and Mairitanian case-studies. Le Bulletin des Séances de l'Académy Royale des Sciences d'Outre-Mer 48, 487–511.

Dahdouh-Guebas, F., Van Pottelbergh, I., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on retrospective remote sensing, social surveys, and distribution of trees. Mar. Ecol. Prog. Ser. 272, 77–92.

Dahdouh-Guebas, F., Hettiarachchi, S., Lo Seen, D., Batelaan, O., Sooriyarachchi, S., Jayatissa, L.P., Koedam, N., 2005a. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. Curr. Biol. 15, 579–586.

Dahdouh-Guebas, F., Van Hiel, E., Chan, J.C., Jayatissa, L.P., Koedam, N., 2005b. Qualitative distinction of congeneric and introgressive mangrove species in mixed patchy forest assemblages using high spatial resolution remotely sensed imagery (IKONOS). Syst. Biodivers. 2, 113–119.

Dahdouh-Guebas, F., Koedam, N., 2008. Long-term retrospection on mangrove development using transdisciplinary approaches: A review. Aquat. Bot. 89, 80–92.

Davis, S.M., Childers, D.L., Lorenz, J.J., Wanless, H.R., Hopkins, T.E., 2005. A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. Wetlands 25, 832–842.

DeAngelis, D.L., Gross, L.J., 1992. Individual-based Models and Approaches in Ecology. Chapman and Hall, New York.

DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. Annu. Rev. Ecol. Evol. Syst. 36, 147–168.

Denslow, J.S., Ellison, A.M., Sanford, R.E., 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. J. Ecol. 86, 597–609.

Doyle, T.W., 1981. The role of disturbance in the gap dynamics of montane rain forest: an application of a tropical forest succession model. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer, New York, Heidelberg, Berlin, pp. 56–73.

Doyle, T.W., 1998. Chapter 6: modeling global change effects on coastal forests. In: Guntenspergen, G.R., Vairin, B.A. (Eds.), Vulnerability of coastal wetlands in the Southeastern United States: climate change research results, 1992–1997, BSR 1998-0002. Lafayette, USGS/BRD. Biological Science Report, pp. 67–79.

Doyle, T.W., Girod, G.F., 1997. The frequency and intensity of Atlantic hurricanes and their influence on the structure of south Florida mangrove communities. In: Diaz, H.F., Pulwarty, R.S. (Eds.), Hurricane, Climate and Socioeconomic Impact. Springer Verlag, New York, NY, USA, pp. 55–65.

Doyle, T.W., Smith, T.J., Robblee, M.B., 1995. Wind damage effects of Hurricane Andrew on mangrove communities along the southwest coast of Florida, USA. J. Coast. Res. 21, 159–168.

Doyle, T.W., Girod, G.F., Books, M.A., 2003. Chapter 12: modeling mangrove forest migration along the southwest coast of Florida under climate change. In: Ning, Z.H., Turner, R.E., Doyle, T.W., Abdollahi, K. (Eds.), Integrated Assessment of the Climate Change Impacts on the Gulf Coast Region. GRCCC and LSU Graphic Services, Baton Rouge, LA, pp. 211–221.

Duke, N.C., 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. Wetlands Ecol. Manage. 9, 257–269.

Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecol. Biogeogr. Lett. 7, 27–47.

Duke, N.C., Bell, A.M., Pederson, D.K., Roelfsema, C.M., Nash, S.B., 2005. Herbicides implicated as the cause of severe mangrove dieback in the Mackay region, NE Australia: consequences for marine plant habitats of the GBR World Heritage Area. Mar. Pollut. Bull. 51, 308–324.

Dunning, J.B., Stewart, D.J., Danielson, B.J., Nonn, B.R., Root, T.L., Lamberson, R.H., Stevens, E.E., 1995. Spatially explicit population models: current forms and future uses. Ecol. Appl. 5, 3–11.

Ellison, A.M., 2002. Macroecology of mangroves: large-scale patterns and process in tropical coastal forests. Trends Ecol. Evol. 16, 181–194.

Ellison, A.M., Mukherjee, B.B., Karim, A., 2000. Testing patterns of zonation in mangroves: scale dependence and environmental correlates in the Sundarbans of Bangladesh. J. Ecol. 88, 813–824.

Feller, I.C., McKee, K.L., 1999. Light-gap creation in a Belizean red-mangrove forest by a wood-boring insect. Biotropica 31, 607–617.

Feller, I.C., McKee, K.L., Whigham, D.F., Neill, J.P., 2003a. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62, 145–175.

Feller, I.C., Whigham, D.F., McKee, K.L., Lovelock, C.E., 2003b. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134, 405–414.

Felton, A., Felton, A.M., Wood, J., Lindenmayer, D.B., 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. For. Ecol. Manage. 235, 186–193.

Field, C.D., 1998. Rehabilitation of mangrove ecosystems: an overview. Mar. Pollut. Bull. 37, 383–392.

Field, C.D., 1999. Mangrove rehabilitation: choice and necessity. Hydrobiologia 413, 47–52.

Fromard, F., Puig, H., Mougin, E., Marty, G., Bétoulle, J.L., Cadamuro, L., 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115, 39–53.

Fromard, F., Vega, C., Proisy, C., 2004. Half a century of dynamic coastal change affecting mangrove shorelines of French Guiana. A case study based on remote sensing data analyses and field surveys. Mar. Geol. 208, 265–280.

Glaser, M., 2003. Interrelations between mangrove ecosystem, local economy and social sustainability in Caeté Estuary, North Brazil. Wetlands Ecol. Manage. 11, 265–272.

Gosz, J.R., 1992. Gradient analysis of ecological change in time and space: implications for forest management. Ecol. Appl. 2, 248–261.

Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecol. Model. 115, 129–148.

Grimm, V., Railsback, S.F., 2005. Individual-based Modelling and Ecology. Princeton University Press, Princeton, NY.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T.K., Heinz, S., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Peer, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabøg, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115–126.

Hernández-Cornejo, R., Koedam, N., Ruiz Luna, A., Troell, M., Dahdouh-Guebas, F., 2005. Remote sensing and ethnobotanical assessment of the mangrove forest changes in the Navachiste-San Ignacio-Macapule lagoon complex, Sinaloa, Mexico. Ecol. Soc. 10, 16.

Hölker, F., Breckling, B., 2002. Concepts of scales, hierarchies and emergent properties in ecological models. In: Hölker, F. (Ed.), Scales, Hierarchies and Emergent Properties in Ecological Models. Peter Lang, Frankfurt, pp. 7–27.

Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. BioScience 38, 682–691.

Huston, M.A., 1994. Biological Diversity. Cambridge University Press, Cambridge.

Kairo, J.G., Dahdouh Guebas, F., Gwada, P.O., Ochieng, C., Koedam, N., 2002. Regeneration status of mangrove forests in Mida Creek, Kenya: a compromised or secured future? Ambio 31, 562–568.

Keane, R.E., Austin, M., Dahlmann, R., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A., Wyckoff, P., 2001. Plant mortality in gap models. Climatic Change 51, 509–540.

Khurana, E., Singh, J.S., 2006. Impact of life-history traits on response of seedlings of five tree species of tropical dry forest to shade. J. Trop. Ecol. 22, 653–661.

Komiyama, A., Ogino, K., Aksornkoae, S., Sabhasri, S., 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. J. Trop. Ecol. 3, 97–108.

Komiyama, A., Ong, J.E., Poungparn, S., 2008. Allometry, biomass, and productivity of mangrove forests: A review. Aquat. Bot. 89, 128–137.

Kovacs, J.M., Wang, J., Blanco-Correa, M., 2001. Mapping disturbances in a mangrove forest using multi-date Landsat TM imagery. Environ. Manage. 27, 763–776.

Krauss, K.W., Doyle, T.W., Twilley, R.R., Smith, T.J., Whelan, K.R.T., Sullivan, J.K., 2005. Woody debris in the mangrove forests of south Florida. Biotropica 37, 9–15.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: A review. Aquat. Bot. 89, 105–127.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquat. Bot. 89, 201–219.

Lewis III, R.R., 1982. Mangrove forests. In: Lewis, III, R.R. (Ed.), Creation and Restoration of Coastal Plant Communities. CRC Press, Boca Raton, Florida, pp. 154–171.

Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. For. Ecol. Manage. 73, 157–175.

Lopez-Hoffman, L., Anten, N.P.R., Martinez-Ramos, M., Ackerly, D.D., 2007. Salinity and light interactively affect neotropical mangrove seedlings at the leaf and whole plant levels. Oecologia 150, 545–556.

Lovelock, C.E., Feller, I.C., 2003. Photosynthetic performance and resource utilization of two mangrove species coexisting in a hypersaline scrub forest. Oecologia 134, 455–462.

Lucas, R.M., Ellison, J.C., Mitchel, A., Donnelly, B., Finlayson, M., Milne, A.K., 2002. Use of stereo aerial photography for quantifying changes in the extent and height of mangroves in tropical Australia. Wetlands Ecol. Manage. 10, 159–173.

Lugo, A.E., 1980. Mangrove ecosystems: successional or steady state? Trop. Succession 12, 65–72.

Lugo, A.E., 1997. Old-growth mangrove forests in the United States. Conserv. Biol. 11, 1–20.

Lugo, A.E., 2000. Effects and outcomes of Caribbean hurricanes in a climate change scenario. Sci. Total Environ. 262, 243–251.

Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. 5, 39–64.

Lugo, A.E., Sell, M., Snedaker, S.C., 1976. Mangrove ecosystem analysis. In: Pattern, B.C. (Ed.), System Analysis and Simulation in Ecology. Academic Press, Inc., New York, pp. 113–145.

Macintosh, D.J., Ashton, E.C., Havanon, S., 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. Estuar. Coast. Shelf Sci. 3, 331–345.

Matthijs, S., Tack, J., Van Speybroeck, D., Koedam, N., 1999. Mangrove species zonation and soil redox state, sulfide concentration and salinity in Gazi Bay (Kenya), a preliminary study. Mangroves Salt Marshes 3, 243–249.

McKee, K.L., 1993. Soil physicochemical patterns and mangrove species distribution—reciprocal effects? J. Ecol. 81, 477–487.

McKee, K.L., Mendelssohn, I.A., Hester, M.W., 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. Am. J. Bot. 5, 1352–1359.

Menezes, M., Berger, U., Worbes, M., 2003. Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, North Brazil. Wetlands Ecol. Manage. 11, 233–242.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian tree species. For. Ecol. Manage. 113, 109–123.

Moorcroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: the ecosystem demography model. Ecol. Monogr. 71, 557–585.

Mueller-Dombois, D., 1991. The mosaic theory and the spatial dynamics of natural dieback and regeneration in Pacific forests. In: Remmert, H. (Ed.), The Mosaic-cycle Concept of Ecosystems. Springer, Berlin, Heidelberg, New York, pp. 46–60.

Pacala, S., Canham, C.D., Silander, J., 1993. Forest models defined by field measurements. I. The design of a northeastern forest simulator. Can. J. For. Res. 23, 1980–1988.

Perry, G.L.W., Enright, N.J., 2006. Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. Prog. Phys. Geogr. 30, 47–72.

Pickett, S.T.A., Kolasa, J., Armesto, J.J., Collins, S.L., 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54, 129–136.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Piou, C., Feller, I.C., Berger, U., Chi, F., 2006. Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane. Biotropica 38, 365–374.

Piou, C., Berger, U., Hildenbrandt, H., Feller, C.I., in press. Modeling the effect of hurricane disturbances on mangrove forest diversity. J. Veg. Sci.

Piou, C., Berger, U., Hildenbrandt, H., Grimm, V., Diele, K., D'Lima, C., 2007. Simulating cryptic movements of a mangrove crab: recovery phenomena after small scale fishery. Ecol. Model. 205, 110–122.

Piou, C., 2007. Patterns and individual-based modeling of spatial competition within two main components of Neotropical mangrove ecosystems. Ph.D. Thesis. University of Bremen, Germany, p. 246.

Ramachandran, S., Anitha, S., Balamurugan, V., Dharanirajan, K., Vendhan, K.E., Divien, M.I.P., Vel, A.S., Hussain, I.S., Udayaraj, A., 2005. Ecological impact of tsunami on Nicobar Islands (Camorta, Katchal, Nancowry and Trinkat). Curr. Sci. 89, 195–200.

Ray, S., Ulanowicz, R.E., Majee, N.C., Roy, A.B., 2000. Network analysis of a benthic food web model of a partly reclaimed island in the Sundarban mangrove ecosystem in India. J. Biol. Syst. 8, 263–278.

Remmert, H., 1991. The mosaic-cycle concept of ecosystems: an overview. Ecol. Stud. 85, 1–21 Springer.

Reynolds, J.H., Ford, E.D., 2005. Improving competition representation in theoretical models of self-thinning: a critical review. J. Ecol. 93, 362–372.

Rivera-Monroy, V.H., Twilley, R.R., Boustany, R.G., Day Jr., J.W., Vera-Herrera, F., Ramirez, M.D.C., 1995. Direct denitrification in mangrove sediments in Terminos Lagoon, Mexico. Mar. Ecol. Prog. Ser. 126, 97–109.

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., Twilley, R.R., Medina, E., Moser, E.B., Botero, L., Francisco, A.M., Bullard, E., 2004. Spatial variability of soil nutrients in disturbed riverine mangrove forests at different stages of regeneration in the San Juan River estuary, Venezuela. Estuaries 27, 44–57.

Ross, M.S., Ruiz, P.L., Sah, J.P., Reed, D.L., Walters, J., Meeder, J.F., 2006. Early post-hurricane stand development in Fringe mangrove forests of contrasting productivity. Plant Ecol. 185, 283–297.

Roth, L.C., 1992. Hurricanes and mangrove regeneration: effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. Biotropica 24, 375–384.

Scholander, P.F., Hammel, H.T., Hemmingson, E., Garey, W., 1962. Salt balance in mangroves. Plant Physiol. 37, 722–729.

Sherman, R.E., Fahey, T.J., Battles, J.J., 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. J. Ecol. 88, 165–178.

Sherman, R.E., Fahey, T.J., 2001. Hurricane impacts on a mangrove forest in the Dominican Republic: damage patterns and early recovery. Biotropica 33, 393–408.

Shugart, H.H., 1984. A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models. Springer-Verlag, New York.

Simard, M., Zhang, K., Rivera-Monroy, V.H., Ross, M.S., Ruiz, P.L., Castaneda-Moya, E., Twilley, R.R., Rodriguez, E., 2006. Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. Photogramm. Eng. Rem. Sens. 72, 299–311.

Smith III, T.J., 1992. Forest structure. In: Robertson, A.J., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 101–136.

Smith III, T.J., Robblee, M.B., Wanless, H.R., Doyle, T.W., 1994. Mangroves, hurricanes, and lightning strikes. BioScience 44, 256–262.

Thampanya, U., Vermaat, J.E., Duarte, C.M., 2002. Colonization success of common Thai mangrove species as a function of shelter from water movement. Mar. Ecol. Progr. Ser. 237, 111–120.

Thampanya, U., 2006. Mangroves and sediment dynamics along the coasts of southern Thailand. Dissertation. Wageningen University.

Thom, B.G., 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. J. Ecol. 55, 301–343.

Thom, B.G., 1984. Coastal landforms and geomorphic processes. In: Snedaker, S.C., Snedaker, J.G. (Eds.), The Mangrove Ecosystem: Research Methods. UNESCO, Paris, France, pp. 3–17.

Tilman, D., 1988. Dynamics and Structure of Plant Communities. Princeton University Press.

Twilley, R.R., 1995. Properties of Mangrove Ecosystems Related to the Energy Signature of Coastal Environments. University Press of Colorado Maximum Power, pp. 43–62.

Twilley, R.R., 1997. Mangrove wetlands. In: Messina, M., Connor, W. (Eds.), Southern Forested Wetlands: Ecology and Management. CRC Press, Boca Raton, Florida, pp. 445–473.

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 Pollut. 64, 265–288.

Twilley, R.R., Chen, R., Rivera-Monroy, V.H., 1999a. Formulating a model of mangrove succession in the Caribbean and Gulf of Mexico with emphasis on factors associated with global climate change. Curr. Top. Wetland Biogeochem. 3, 118–141.

Twilley, R.R., Rivera-Monroy, V.H., Chen, R., Botero, L., 1999b. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. Mar. Pollut. Bull. 37, 404–419.

Twilley, R.R., Rivera-Monroy, V.H., 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. J. Coast. Res. 40, 79–93.

Urban, D.L., O'Neill, R.V., Shugart, H.H., 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. BioScience 37, 119–127.

Vega-Cendejas, M.-E., Arreguin-Sanchez, F., 2001. Energy fluxes in a mangrove ecosystem from coastal lagoon in Yucatan peninsula, Mexico. Ecol. Model. 20, 119–133.

Verheyden, A., De Ridder, F., Schmitz, N., Beeckman, H., Koedam, N., 2005. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. New Phytol. 167, 425–435.

Walters, B.B., 2005. Patterns of local wood use and cutting of Philippine mangrove forests. Econ. Bot. 59, 66–76.

Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquat. Bot. 89, 220–236.

Wang, L., Sousa, W.P., Gong, P., Biging, G.S., 2004. Comparison of IKONOS and QuickBird images for mapping mangrove species on the Caribbean coast of Panama. Rem. Sens. Environ. 91, 432–440.

Ward, G.A., Smith, T.J., Whelan, K.R.T., Doyle, T.W., 2006. Regional processes in mangrove ecosystems: spatial scaling relationships, biomass, and turnover rates following catastrophic disturbance. Hydrobiologia 569, 517–527.

Whelan, K.R.T., 2005. The successional dynamics of lightning-initiated canopy gaps in the mangrove forests of Shark River, Everglades National Park, USA. Ph.D. Thesis. Florida International University.

Wolanski, E., 1992. Hydrodynamics of mangrove swamps and their coastal waters. Hydrobiologia 247, 141–161.

Wolff, M., 2006. Biomass flow structure and resource potential of two mangrove estuaries: insights from comparative modeling in Costa Rica and Brazil. Revista de Biologia Tropical 54, 69–86.

Woodroffe, C., 1992. Mangrove sediments and geomorphology. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, DC, pp. 7–42.

Wullschleger, S.D., Jackson, R.B., Currie, W.S., Friend, A.D., Luo, Y., Mouillot, F., Pan, Y., Shao, G.F., 2001. Below-ground processes in gap models for simulating forest response to global change. Climatic Change 51, 449–473.