STRUCTURE, FUNCTION AND MANAGEMENT OF MANGROVE ECOSYSTEMS

Jin Eong Ong & Wooi Khoon Gong



ISME Mangrove Educational Book Series No. 2

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International Society for Mangrove Ecosystems (ISME), c/o Faculty of Agriculture, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa, 903-0129 Japan



International Society for Mangrove Ecosystems

International Tropical Timber Organization

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Cover photographs:

General view of the Merbok mangrove, Malaysia

Canopy of a mature mangrove forest in Matang, Malaysia

Silvered langur or silvered leaf monkey with offspring

Sesarmid crab staying above the water during high tide

Photo credits: all photographs are by the first author unless otherwise stated.

Contents

ISME and ITTO		
About the Authors	iv	
Preface	V	
Acknowledgements	V	
Note from ISME	vi	
Chapter 1 INTRODUCTION	1	
Chapter 2 ECOSYSTEM STRUCTURE	7	
2.1 GEOMORPHIC FACTORS Tides and Tidal Inundation Sedimentation and Erosion Sea Level Change Soils	7 7 8 11	
2.2 BIOTIC FACTORS	13	
Plant Adaptations Adaptation to the Saline Environment Salt exclusion Salt-secreting glands Salt accumulation Adaptation to the Soft Substrate/Aquatic Environment Vivipary and cryptovivipary Water dispersion of seeds and propagules Stilt and buttress roots Adaptation to Anaerobic Conditions Lenticels Pneumatophores Animal Adaptations Avoidance Adaptation to desiccation Adaptation to anaerobic conditions Opportunistic detritivory	13 13 13 13 14 14 14 14 15 15 17 17 17 18 21 21 23 23 24	
Chapter 3 ECOSYSTEM FUNCTION	27	
3.1 PRODUCERS	27	
Primary Production by Vascular Plants Gross Primary Production Net Primary Production <i>Plant biomass increment</i> <i>Litter production</i> Primary Production of Algae	27 28 28 28 32 32	

3.2 CC	DNSUMERS (HERBIVORES AND CARNIVORES)	32
The Gra Decom <i>Fra Lea</i> <i>Sap</i> The De Export a	azing Food Chain posers agmentation aching prophytic activity trital Food Chain and Burial	33 36 36 36 36 37 38
Chapte	r 4 SOCIO-ECONOMIC AND MANAGEMENT CONSIDERATIONS	39
4.1 M	angrove goods and services	39
Mangro Tir Oti Fis Na Fic Mangro Ma Sec Bir Ma Sec Ecc	ve Goods mber her forest products h tural cockles pating cage aquaculture ve Services intenance of channel depth diment accretion and coastal protection d sanctuary/migratory stops ingroves and adjacent coastal fisheries questration of atmospheric carbon dioxide ptourism	39 39 39 42 42 43 43 43 43 44 45 46 48
4.2 VA	LUE OF MANGROVES	54
Monetary Value of Mangroves Sustainable Use Management Unsustainable and Conversional Use		
Refere	nces	67
Box 3.1	Estimating the Biomass of a Tree	30
Box 3.2	Primate Herbivores of the Mangroves of Borneo	34
Box 4.1	CDM, REDD and Blue Carbon	47
Box 4.2	Kuala Gula Bird Sanctuary in Matang	52
Box 4.3	Matang Mangrove Management	55
Box 4.4	Lightning Gaps in Mangroves?	60

ISME and ITTO

ISME

The International Society for Mangrove Ecosystems (ISME) is an international non-profit and non-governmental scientific society established in August 1990. With its headquarters in Okinawa, Japan, ISME was certified as a Foundation in 1992 by the Japanese Law of Foundation. In 2003, under a new Japanese law of promoting specified non-profit activities, ISME was registered as a Non-Profit Organization (NPO). Revised at the Eighth General Assembly in 2012, the Statutes of ISME stipulate that 'the Society shall collect, evaluate and disseminate information on mangrove ecosystems', and 'shall promote international cooperation'. ISME has been carrying out its activities at the global level through: a) application of knowledge to particular situations, b) training and education, and c) exchange of necessary information. Activities of the society have been supported with collaboration and links by a number of other organizations, universities, research institutes and local communities. Currently, ISME's membership includes 40 institutions and over 1,150 individuals from 92 countries.

ITTO

The International Tropical Timber Organization (ITTO) is an intergovernmental organization promoting the conservation and sustainable management, and the use and trade of tropical forest resources. Its 65 members represent most of the world's tropical forests and 90% of the global tropical timber trade. ITTO develops internationally agreed policy documents to promote sustainable forest management and forest conservation, and assists tropical member countries to adapt such policies to local circumstances and to implement them in the field through projects. In addition, ITTO collects, analyses and disseminates data on the production and trade of tropical timber, and funds projects are funded by voluntary contributions, mostly from consumer member countries. Since it became operational in 1987, ITTO has funded more than 800 projects, pre-projects and activities valued at more than USD 350 million. The major donors are the governments of Japan, Switzerland, EU and USA.

About the Authors

ONG Jin Eong and GONG Wooi Khoon were anchor members of the Mangrove Ecosystem Research Group, Universiti Sains Malaysia. The group was formed in the mid-1970s through a very modest seed grant from their University. They went on to procure other research grants including those from the International Development and Research Centre (IDRC) of Canada, the Australian International Development Assistance Bureau (AIDAB via the ASEAN-Australia Cooperative Project on Marine Science) and the Netherlands Foundation for Advancement of Tropical Research (WOTRO), as well as Malaysian Government grants (IRPA) under the Fifth and Sixth Malaysian Plans.

The group's *modus operandi* was to work on the mangrove ecosystem, mainly *in situ*, with the main aim of closing the carbon (as well as nitrogen and phosphorus) budget. Towards this end, the group conducted a whole range of different projects including felling trees and digging roots to obtain allometric regressions; building tree towers to measure rates of photosynthesis in the canopy, and sitting in small boats along the estuary for 31 continuous tidal cycles to estimate water, salt and material fluxes. Some of these were major logistic exercises involving up to 60 staff and students for two weeks at a time. Thanks to their willing and cheerful assistance, the group has some unique time-series data sets. Comprising mainly ecologists, the group has worked with plant eco-physiologists, physical oceanographers, mathematical modellers and economists from Australia, Britain, Canada, Japan, Southeast Asia and the USA, as well as locally. As important as doing interesting and fun science, the group made good friends all over the world.

ONG Jin Eong

Dr. Ong, the leader of the Group, obtained his Ph.D. from the University of Tasmania in Australia. He served on the editorial boards of BIOTROPICA, Asian Marine Biology, and Mangroves and Salt Marshes. He was a member of the Malaysian National Science Research and Development Council, and the Joint UN Group of Experts on the Scientific Aspects of Marine Protection (GESAMP).

GONG Wooi Khoon

Dr. Gong obtained her Ph.D. from the University of Aberdeen in Scotland. On returning to Universiti Sains Malaysia, she started research on Dipterocarp forests before joining the Mangrove Ecosystem Research Group. Besides the research and teaching (both at the undergraduate and postgraduate levels), Gong enjoyed her various sabbaticals including those at Oxford University (Senior Visiting Fellow of Linacre College), Harvard University (as Charles Bullard Fellow), and the Research Institute for Humanity and Nature in Kyoto, Japan (as Visiting Professor).

Preface

This book *Structure, Function and Management of Mangrove Ecosystems* is the second in a trilogy to be published simultaneously. The others are *Continuing the Journey Amongst Mangroves* by Barry Clough, and *Useful Products from Mangrove and other Coastal Plants* by Shigeyuki Baba, Hung Tuck Chan and Sanit Aksornkoae.

This book is about mangrove plants and animals that colonise the main part of the intertidal zone in the tropics and subtropics. It highlights the structure, function, state of health, and as importantly, the sustainable economic and ecological management of mangrove forests.

This book is not written for the professionals but aimed more at semi-professionals, students and those who need an introduction to mangroves at a higher than just a superficial treatment. The confusion with rehabilitation of mangroves after the 2004 Indian Ocean tsunami strongly suggests that such a book would fulfil a need. The authors also wish to share their considerable experience working (mainly in the field in hands-on situations) in some of the most biologically diverse and luxuriant mangroves in the world.

It is not the intention of this book to provide a highly technical review of the subject. As such, the references are not extensive but enough to point the way for further reading. This makes for easier reading. This book is also structured in such a way that the photographs, with their own captions, can be read independently from the text. The boxes provide further details and need not be read with the text or photographs.

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ISME is indebted to the Project Technical Committee, comprising members of the Executive Committee, for their support of the project, and critical comments and sound advice on the chapters of the books. The contributions of Prof. Sanit Aksornkoae, Ambassador Noboru Nakahira, Prof. François Blasco, Prof. Norman Duke, Prof. Salif Diop and Dr. Mami Kainuma are very much appreciated. The commendable efforts of Dr. Steve Johnson as the Project Manager from ITTO, Dr. Hung Tuck Chan as the Project Coordinator and Book Editor, and Ms. Nozomi Oshiro as the Project Administrator have enabled the smooth implementation of the project activities. Gratitude goes to the Sabah Forestry Department in Sandakan, Sabah for collaborating with ISME, and for providing the Rainforest Discovery Centre as venue for the launching of the books and seminar of the project.

Under the project, three books representing the beginning of the *ISME Mangrove Educational Book Series* are produced. They are written, published and launched in commemoration of Prof. Shigeyuki Baba, the Executive Director of ISME, who will be retiring from University of the Ryukyus in March 2013.

Chapter 1 INTRODUCTION

The littoral or intertidal zone defines the interface between land and sea. This is a zone of land that is intermittently inundated to varying degrees by tidal waters. This is also generally known as the coastline and coasts may be divided by the nature of their substrate, from rocks (the rocky shore ecosystem) to sand (the sandy beach ecosystem) to mud. The upper reaches of beaches are often vegetated (strand vegetation) but most of this often narrow strip of vegetation is beyond the reach of all but exceptionally high tides. In the muddy coasts, vegetation almost invariably establishes, especially where there is a supply of freshwater from rivers or subterranean sources. In such situations, either mangrove (in the tropics, subtropics, and into the temperate areas where there are no ground frosts) or salt marsh ecosystems establish. These two ecosystems are characterised by salt-tolerant terrestrial plants (halophytes) with the necessary adaptations to live in soft, often anaerobic substrates that are subjected to varying degrees of tidal inundation and salinities up to full strength seawater. Sea grasses are sometimes also found in the infralittoral zone: they are marine angiosperms, usually found completely submerged (but having a certain tolerance to exposure). At the supra-littoral upper shore, truly terrestrial plants are also present. Also sometimes found in this supra-littoral zone (in places with a marked seasonal rainfall or where evaporation usually exceeds precipitation), saltpans are formed. These are colonised by a group of plants that can tolerate hyper-saline (saltier than seawater) conditions.

Thus, the mangrove and salt marsh ecosystems are dominant coastal ecosystems, the former in the tropics and subtropics (and even extending into the temperate areas) and the latter mainly in the temperate region. Apart from being very productive, these ecosystems play important roles in coastal protection, supporting their own and purportedly, adjacent coastal fisheries, and providing timber and a host of other natural products. Mangroves constitute an estimated 2% of the earth's land surface and can be considered rare. They are also highly threatened, with an estimated loss of at least 50% in the second half of the 20th Century; which places these ecosystems under the 'headed for extinction' category of the International Union for the Conservation of Nature and Natural Resources (Polidoro et al., 2010; Spalding et al., 2010).

Mangroves are a group of vascular plants that have special morphological, physiological and other non-visible adaptations to live in a saline intertidal environment dominated by low dissolved oxygen or sometimes anoxic fine sediments. These plants, together with their complement of microorganisms and animals, form the mangrove ecosystem. The term mangrove thus refers both to the plants themselves as well as to the ecosystem. Often, plants which occur in the non-mangrove ecosystem (usually in strand or beach vegetation) and with none or only a few of these morphological adaptations, are also found in the mangrove forests.

Thus mangrove plants are sometimes classified as either true mangroves or mangrove associates (Tomlinson, 1986). True mangroves are plants with many morphological adaptations and found almost exclusively in the mangrove ecosystem. Nonetheless, like any classification system, there will be contention as to whether some particular species should be true mangroves or mangrove associates. No classification system is perfect and Tomlinson (1986) had himself admitted: 'Of course, the groups are not sharply circumscribed and the assessment is somewhat subjective, since there is a continuum of possibilities.'

For example, *Excoecaria agallocha* has only a single morphological adaptation (lenticels) but because it is rarely found in other coastal ecosystems, it is considered by most to be a true mangrove (however, please refer to Wang et al., 2010). Yet there are some who do not consider *Nypa fruticans* to be a true mangrove despite its having viviparous fruits because it occurs extensively in freshwater, a distinct ecosystem on its own.



Bole of *Excoecaria agallocha* with corky lenticels (left). The species is dioecious (with male and female trees) and produces a milky sap, which can cause blistering and temporary blindness. Leaves turn bright red before dropping. A bunch of fruits (infructescence) of *Nypa fruticans* (right). This is a palm that grows in freshwater, usually in the tidal part of the estuary, and the fruits are cryptoviviparous.

Diospyros ferrea is considered by Tomlinson (1986) to be a mangrove associate. This, like the other *Diospyros* species or varieties found in back mangroves do not have any of the characteristics that make them true mangroves. They are only occasionally found (but not exclusively) in back mangroves. Yet *Diospyros littorea* (considered a variety of *Diospyros ferrea*) is listed as a true mangrove in the World Atlas of Mangroves (Spalding et al., 2010) and in the IUCN Mangrove Red List (Polidoro et al., 2010). Both these lists were based on Duke (2006).



Diospyros ferrea, from the Andaman coast of Thailand (fruits shown here) does not exhibit any visible morphological adaptations to living in the mangrove ecosystem. It is also not exclusively found in mangroves so, at best, can only be considered a mangrove associate. Yet the species *Diospyros littorea* (a variety of *Diospyros ferrea*) appears as a true mangrove on the IUCN list.

To further muddy the situation, we ask here, why the salt tolerant as well as viviparous *Cryptocoryne ciliata* is rarely on mangrove lists? Surely, it is as deserving as *Diospyros ferrea* or the other back mangrove *Diospyros* species or varieties to be listed at least as a mangrove associate? Or is it because Tomlinson (1986) excluded herbs as mangroves? Perhaps, recent studies like that of Wang et al. (2010) could help clarify the muddy waters!

The mangrove ecosystem is ephemeral in terms of its location, in that it moves in response to changes in sea level. The fact that mangrove plants have existed for millions of years, through numerous glacial and interglacial periods shows that this ecosystem is well adapted to global climate changes. Since *Homo sapiens* is a very recent inhabitant of Earth, their impact was not noticeable in the last shift from glacial to the present interglacial but their ability to change the environment, especially in the past couple of hundred years, has been profound. It is thus not moot as to whether this ecosystem can adequately respond to global changes brought on by *Homo sapiens*. Equally important is to consider what actions should be taken to minimise damage to this ecosystem.



A riverine grove of *Cryptocoryne ciliata* growing amongst true mangroves such as *Sonneratia caseolaris* and *Nypa fruticans* (top). The spathe or flower (bottom left) and a newly settled plumina (bottom right) of the species. Often cultivated as an aquarium plant, it is viviparous and occurs in the upper part of the estuary where the water is brackish.

Where development along the coasts has occurred, the land behind the landward edge of mangroves have usually been converted to alternate uses (e.g. agriculture or industrial land); and should there be an increase in sea level, there will be nowhere for mangroves to move to. The chances are infinitely better should sea level fall, because there are very fewer areas where the seaward side of mangroves have been developed. The present likely scenario is for the sea level to rise (predicted as a consequence of increases in atmospheric carbon dioxide and other greenhouse gases attributed to anthropogenic activities). So, based on present forecasts, many mangroves may drown as a result of the predicted sea-level rise. It must be pointed out that whilst it is true that the concentration of atmospheric carbon dioxide has risen alarmingly since the industrial revolution, it is not completely certain that this has resulted in global warming, which in turn would cause sea levels to rise globally. Some important feedback mechanisms are not clearly understood. Although there may be signals, these are still not completely clear-cut. There is also evidence that the present interglacial peaked a few thousand years ago and that the trend for sea-level rise reversed. On the stable Sunda Shelf, for instance, sea level has fallen some 3-5 metres in the last 4,000 years (Geyh et al., 1979). The jury is still out on this question.

There are enough reasons why we should conserve our rare and useful mangrove ecosystems, yet they (because the bulk of the world's mangroves occur in developing countries) are still being destroyed at a rate that places them in the endangered category. There is still a lot of science to be done but time has almost run out. It is time to apply the precautionary principle.



Extinction is forever: *Bruguiera hainesii*, (flowers shown here) is the rarest of all mangrove species. It is categorised in the IUCN Mangrove Red List as 'Critically Endangered', with only some 250 trees in existence. These photos are from a single tree in Penang, Malaysia; probably washed in by the 2004 Indian Ocean tsunami.

Granted, it is not easy for developing countries with mushrooming human populations to conserve for posterity when it is uncertain where the next meal is coming from, but not all developing countries are in such dire straits. Also, much of the destruction and degradation is not so much a result of need as of greed (the mangrove woodchips/rayon industry, for example). The problem is the low value that has been placed on mangroves and our flawed economic system in its consideration (or lack thereof) of ecological values. There is a need for a paradigm shift, and towards this, there is urgent need for ecologists to work very much more closely with economists – not merely to put values on goods and services but to evolve an ecologic-economic system that is more socially just and that will result in the sustainable use of ecosystems. This is indeed the challenge of the new millennium; if it is not met, humankind may not survive to see the next.

This book is about plants (mangroves) and some of the animals that colonise the main part of the intertidal range in the tropics and subtropics (where ground frosts do not occur). It is about the structure, function, state of health, and sustainable economic and ecological management of the mangrove ecosystem.

Authors' Note: Together, we have some 80 years of muddling in mainly Southeast Asian and Australasian mangroves. Whilst we admit our bias (from our examples and photos), we make no apologies, just a declaration; so this book can be read in the proper perspective.



False colour satellite (Landsat) imagery (top left) and up-to-date Google Earth imagery (top right) of the Merbok mangrove in Malaysia. More details (including identification down to the genus level) can be obtained from aerial photographs (bottom). An aerial survey provides a quick overview of the nature and condition of mangroves that are not easily visible from the ground.



A predominantly *Rhizophora apiculata* forest of the Merbok mangrove, Malaysia (top). This is one of the most species diverse mangroves globally but is also highly endangered (Ong, 2003). Looking up into the canopy of a mature mangrove forest in Matang, Malaysia (bottom). The canopy of the 40-year-old forest has an almost full cover with leaf area index of 4–5.

Chapter 2

ECOSYSTEM STRUCTURE

2.1 GEOMORPHIC FACTORS

In general, tropical coastlines can be broadly divided into rocky shores (usually where the hills come right to the coast, and the rocks and boulders have rolled down the hills into the sea from the process of erosion); sandy beaches (usually on plains subjected to high-energy wave action); and mangroves (small or very extensive plains in sheltered, usually low-energy coasts). Of the three, mangroves extend farthest into the sea (as well as up river) and thus tides play a very important role.

Tides and Tidal Inundation

In order to understand mangroves (since it is present in an intertidal or littoral habitat), it is important to understand tides and the influence of tides (in particular, tidal inundation) on not just the flora and fauna, but also on the sedimentation and erosion processes.

It is not our intention to explain in detail what tides are (reference can be made to basic books or articles on this important phenomenon). Suffice it to say that tides are influenced by celestial bodies, the changes in the phase of the moon, (the celestial body closest to Earth), in particular. Spring tides (when the tidal range is highest) occur during the new and the full moon; and neap tides (when the tidal range is close to its minimum) at around a quarter moon and around a three-quarter moon. The spring tides at certain times of the year may be higher than at others and the highest tides occurs when other planets line up with the moon to produce 'equinoctial' or 'king' tides.

During spring tides, more of the littoral zone is inundated as well as exposed, and during neap tides, less of the intertidal zone is inundated and exposed. This is very important as the degree of tidal inundation influences the presence or absence of particular species of mangroves. Watson (1928) devised a tidal inundation classification scheme that comprised five inundation classes (Table 2.1) and was able to associate each inundation class with the species of mangroves that occurred there. This classification, with its associated mangrove species occurrence, was particularly for the Matang mangrove on the west coast of Peninsular Malaysia but should be applicable to other mangrove areas with some modifications, after on-site observations. This simple concept is very important to understand for those involved in mangrove rehabilitation work. Unfortunately, most of the mangrove rehabilitation projects (not that the tsunami destroyed much mangroves!) after the 2004 Indian Ocean tsunami showed that many of the rehabilitators did not have any idea of this concept.

Sedimentation and Erosion

We have said earlier that mangroves occur on sheltered (most of the time low energy) coasts with fine sediments. Often, these fine sediments are brought down by rivers, and are deposited in estuarine deltaic plains. For example, the biggest single continuous area of mangroves (some 6,000 km²) is seen in the Sundarbans. This huge vegetated deltaic plain was formed by fine sediments discharged by the giant Ganges and Brahmaputra Rivers that flow through India and Bangladesh.

Table 2.1Tidal inundation classes of mangroves and common tree species found (modified from Watson, 1928)			
	Inundation Class	Common Species	
1.	Inundated by all high tides	None, except perhaps Rhizophora mucronata on banks of streams	
2.	Inundated by medium high tides	Avicennia alba, A. marina and Sonneratia alba. Bordering rivers, Rhizophora mucronata predominates	
3.	Inundated by normal high tides (usually the greatest part of the mangrove area)	Most mangroves will grow here. <i>Rhizophora apiculata</i> reaches its optimum and often in pure stands. <i>Bruguiera parviflora</i> and <i>Ceriops</i> also grow well and often in mixture with <i>R. apiculata</i> .	
4.	Inundated by spring tides	This zone is generally too dry for the <i>Rhizophora</i> species but the <i>Bruguiera</i> species (particularly <i>B. gymnorhiza</i> , <i>B. cylindrica</i> and <i>B. parviflora</i>) grow well here, together with the undergrowth ferns, <i>Acrostichum aureum</i> and <i>A. speciosum</i> . <i>Lumnitzera</i> species, <i>Xylocarpus</i> species, <i>Excoecaria</i> agallocha and <i>Ficus</i> microcarpa are also common here.	
5.	Occasionally inundated by exceptional or equinoctial tides	This is known as the back mangrove and is the most species diverse. Many of the species in Class 4 also occur here. Almost pure stands (dotted with <i>Xylocarpus</i> species, <i>Heritiera</i> species and <i>Intsia bijuga</i>) of <i>Nypa fruticans</i> and <i>Oncosperma tigillarium</i> are common. <i>Bruguiera gymnorhiza</i> and <i>B. sexangula</i> also favour this zone. Many mangrove associates and epiphytes often occur here.	

In any coast, the very dynamic processes of sedimentation and erosion (they are essentially two sides of the same coin) are always occurring (even on sheltered coasts where mangroves occur). There will always be areas that are accreting as well as areas that are eroding (even where mangroves are already established). It is important to recognise this important geomorphological process rather than waste money trying to prevent these natural erosion processes with expensive hard engineering solutions. Having a buffer zone a certain fixed distance from the highest tidal limit, that is off limits to any development, is probably the most efficient solution.

Sea Level Change

The recent preoccupation with climate change has resulted in highlighting sea level change. Sea level change is a certainty. What is often less certain is the rate (e.g. millimetres per year) and the direction (rise or fall). A number of factors determine the rate and direction of sea level change. These include:

- i) The expansion⁺ (if there is a rise in temperature) or contraction-(if there is a drop in temperature) of seawater
- ii) Rise- or fall+ of tectonic plates
- iii) Melting+ of glacial ice (but not free-floating ice e.g. icebergs)
- iv) Coastal erosion- and sedimentation+ rates
- v) Extraction+ of subterranean freshwater

The superscript + indicates relative sea level rise and the superscript - indicates relative sea level fall. The change in sea level is thus relative due to these various factors and so is site



specific. Sea level change, due to expansion or contraction of seawater and melting glaciers or growth of glaciers, results in increase or decrease of seawater volume and causes what is known as an eustatic change in sea level. Even if there is no eustatic change, sea level will change if there is tectonic change. It is also difficult to measure eustatic sea level change from just tide gauges alone because other factors (e.g. tectonic) are in play. Recent satellite-based measurements are probably the most reliable but there is only a very short-time series (compared to tidal gauge measurements).



A simple 'tide pole' can measure both tide and sedimentation/erosion (left). The technical problem is to secure the pole in such a way that it is really fixed (in a vertical direction) and not just float in the substrate. Deploying a current meter but this photo also illustrates that sea level is relative (right). On one side of the boat (representing a tectonic plate), sea level rise is observed and on the other side (away from camera) sea level fall is seen.



Excessive numbers of tube wells that extract subterranean ground water will lead to subsistence of land and thus a relative sea level rise. Such tube wells were rampant but are now banned in Bangkok.



A physical barrier used to reduce wave energy and prevent erosion in Samut Songkhram, at the mouth of the Chao Phraya, which flows through Bangkok, Thailand. Such structures (in this case of bamboo poles but others of telephone or electric line concrete poles) become preferred perches for a variety of migrating and resident birds, becoming havens for bird watchers or ecotourists.

One major question here is what are the implications to mangroves with sea level change? First, to put things into a geological (time-scale) perspective, mangroves have survived for millions of years through many glacial or interglacial cycles. For instance, in the last ice age (which was only some 12,000 years back), the sea level was some 120 metres below the present sea level (Peltier, 2002). The relative sea level then rose very rapidly about 4,000 years back, to about 5 metres above and then slowly dropped to the present day sea level, at least for the Straits of Malacca (Geyh et al., 1979; Kamaludin, 1993; Kamaludin & Azmi, 1997). So, in the last few thousand years, we have experienced a falling eustatic sea level. The caveat to this scenario is that there was minimal anthropogenic activity. The present situation is that the landward side of many mangroves are either bunded or have human settlements. With sea level rise, the back mangroves will not be able to migrate landwards (thus, this is also known as the 'coastal squeeze'). The result is that the most landward of the tidal inundation zone disappears and the other inundation zones become more narrow or 'squeezed'. Most of the species in the most inland zone (the most species diverse zone) will thus become extinct in these 'squeezed' mangrove zones. A more comprehensive treatment of this topic can be found in Ong & Tan (2008).

Soils

The substrate that mangroves usually grow on is best referred to as mud (they can also be found on fine, usually carbonate, sediments). There is usually not enough visible structure in this very fine substrate for this mud to be considered as soil, in the true sense of the word.

In the topics, the rainforest forms the climatic climax community. Edaphic (or soil) factors play an important role in changing the form of such forests. The mangrove ecosystem is such an edaphic tropical forest type and here the 'soil' is mud. Another edaphic type is strand or beach vegetation, where the soil is essentially sand.

Mud is essentially a combination of minerals that have been weathered from rocks. There is very little organic matter but as mangroves grow on this substrate, they add organic matter from leaf and root litter as well as other dead parts to the mud. Thus in a mature mangrove forest, the soil organic matter content can be very high, higher than in most other soils. This is partly because the plant parts are buried in either low oxygen (or even anoxic) soil so that the organic matter does not decompose easily. Mangrove soils are thus very effective carbon sinks.

The anoxic condition results in anaerobic sulphur bacteria producing hydrogen sulphide in the deeper anoxic mud. Thus the smell of hydrogen sulphide is seldom noticeable in mangroves, unless the surface soils have been significantly disturbed. Methane (also known as swamp gas) is another product of anaerobic bacterial activity but does not form in mangroves because the sulphate bacteria out competes the methanogenic bacteria in sulphate rich seawater (Kristjansson & Schönheit, 1983) that inundates mangroves.



Most mangrove soils have a high content of organic matter and often, iron. Together with the abundance of sulphate (from seawater), iron pyrites form. When these soils are exposed and oxidised, acid sulphate conditions arise and the water turns acid, making them unsuitable for agriculture or aquaculture.

2.2 BIOTIC FACTORS

The mangrove ecosystem is an intertidal ecosystem which is inundated by seawater and the salinity can vary from 0–35 psu (practical salinity unit) or even higher in certain hyper-saline habitats. The substrate often consists of soft sediments which are waterlogged where low oxygen conditions occur. Plants and animals which live in the mangroves have various adaptations to allow them to survive under these stressful conditions. These adaptations have been described comprehensively in a companion volume to this book by Clough (2013), so only a concise account is given here.

Plant Adaptations

True mangrove species are those which possess structural and physiological adaptations that allow them to live in a saline and low-oxygen environment. Many of the structural adaptations in mangroves are quite spectacular (from massive stilt root systems to propagules up to about a metre in length – both of these are seen in *Rhizophora mucronata*). Adaptations in mangrove plants can be grouped into those dealing with saline conditions, those dealing with the soft substrate and others dealing with anaerobic conditions.

Adaptation to the Saline Environment

Mangroves are halophytes or plants which complete their life cycles in saline waters. However, many species of mangroves can survive in freshwater, suggesting that their ability to live in saline waters gives them a competitive advantage in saline environments. However, some species like *Ceriops decandra* and *Sonneratia alba* could be obligate halophytes (Ball, 1988a) since they showed extremely poor growth and time-dependent vigour in freshwater. Different species vary in their tolerance to salinity, and even within one species, tolerance to salinity can be different depending on the developmental stage of the plant (Ball, 1988b), as seedlings often have food reserves which allow them to grow well even under unfavourable conditions. The optimal salinity for growth of seedlings which have exhausted their food reserves ranges from 10–25% seawater (e.g. Clough, 1984; Ball, 1988a). There are three main ways by which mangroves can deal with salt.

Salt exclusion

One way is to reduce or exclude the uptake of salt. All of the mangroves exclude salt at the roots to some extent but the amount excluded varies and is usually less in the species which possess salt-secreting glands (e.g. Clough, 1984). However, if most of the salt is excluded, it is not possible to obtain a positive osmotic potential. So, another mechanism to increase the osmotic potential within these plants is to increase the content of colloidal organic molecules; from simple sugars to amino acids (Popp 1984a, 1984b). Since these molecules are normal constituents of cells, small increases do not present any physiological tolerance problems. In other words, the osmotic pressure in the plant is generated jointly by ionic and colloidal particles. Hence the plant sap of these plants will have a much greater osmotic pressure than can be accounted for by just its ionic (salt) content. Examples of salt excluders are *Rhizophora*, *Bruguiera* and *Ceriops* of the family Rhizophoraceae.

Salt-secreting glands

Another mechanism for dealing with the excess salt is to excrete the salt taken in via saltsecreting glands. Species in the genera *Acanthus*, *Aegialitis*, *Aegiceras* and *Avicennia* have these salt-secreting glands and crystals of salt are often visible on the leaf surface. Some of the salt carried in the transpiration stream to the leaves is absorbed by the growing tissues for osmoregulation purposes and the excess salt is secreted by the glands so that the ion concentrations are maintained within physiologically tolerable levels (Ball, 1988b). These mangroves are usually more salt tolerant than other mangroves.

Salt accumulation

All mangroves accumulate inorganic ions (Popp 1984a) for the osmoregulation of leaves and other tissues. This is especially so for species which are unable to exclude salt at the root level or excrete salt from salt glands in their leaves. These salt accumulators are species like *Sonneratia, Xylocarpus* and *Excoecaria* that employ the strategy of dropping their leaves (thus eliminating salt and excess organics) when the osmotic particles level becomes intolerable. These three genera also deposit sodium and chloride in the stem and pneumatophore bark.



Leaves of *Avicennia officinalis* showing salt crystals excreted from salt glands on the upper leaf surface (left). Electron micrograph of the salt gland complex of *Acanthus ilicifolius* (right). For more details, please refer to Wong & Ong (1984).

Adaptation to the Soft Substrate/Aquatic Environment

Vivipary and cryptovivipary

Vivipary is a reproductive condition where the seed germinates whilst still attached to the parent plant – these germinated seeds are called propagules. Vivipary is particularly obvious in the Rhizophoraceae. The embryo develops within a small fruit and the embryonic axis, called the hypocotyl, elongates through the surrounding pericarp. The hypocotyl can grow to great length whilst on the parent plant, reaching a metre in *Rhizophora mucronata*. It is often said that these propagules have an advantage in establishing in a soft substrate because the elongated hypocotyl can penetrate the substrate and take root quickly. However, many of the propagules can be seen floating in the mangrove waterways, and will eventually establish away from the parent plant.

Cryptovivipary in *Avicennia*, is similar to vivipary in that the seed also germinates on the parent tree. However, in this case, the developing hypocotyl does not penetrate the pericarp and protrude beyond. The cryptoviviparous seedlings of *Avicennia* can often been seen deposited on the coast (including sandy beaches), and some of these have already developed roots which will help them establish in the new habitat.



Rhizophora mucronata often grow right on the edges of streams (left) as their long propagules (close to a metre) are less susceptible to tidal inundation. The propagules often 'spear' into the mud under the parent trees when they drop. Profuse *Bruguiera parviflora* propagules that are almost ready to drop from the tree (top right). These cryptoviviparous *Avicennia* seedlings grow very quickly as soon as they drop and have tiny Velcro-like hooks to help anchor to larger particles in the mud (bottom right). Their roots were developed after the plant had fallen from the parent tree. This unfortunate seedling was washed up on the beach, probably due to high wave action.

Water dispersion of seeds and propagules

Other mangrove species (in addition to Rhizophoraceae and Avicenniaceae) which have seeds that are water-borne and dispersed away from the parent plant include *Heritiera*, *Xylocarpus* and *Nypa*. The fruit of *Heritiera littoralis* (and *H. fomes*) has a keel. Our observations suggest that often, the keel actually serves as a sail as it is on the upper surface of the floating fruit!

Stilt and buttress roots

Mangrove trees have to adapt to living in soft, muddy habitats and many do so by having aerial roots. *Rhizophora* species are characterised by their prominent stilt roots which diverge from the tree sometimes as high as 2 metres and even up to 3-4 metres as in Gambia (François Blasco, pers. comm.) above ground. These roots can spread and penetrate the soil up to 4 metres from the main stem. These roots thus act much as guy ropes in anchoring the tree in the soft substrate. Other species, like *Heritiera littoralis* and *Xylocarpus granatum*, have very prominent sinuous buttress roots which also help support these plants in the muddy environment.



Heritiera littoralis fruits showing the keel which more likely functions as a 'sail' to aid in dispersal. Since there is no need for stabilisation of the fruit, a keel is redundant.



The stilt roots of *Rhizophora* help to anchor and prop up the tree in a soft substrate (left and top right). Sometimes, aerial roots are developed from the branches to lend additional support to the trees (bottom right).



Massive buttress roots of *Heritiera littoralis* which spread out over large areas and serve to support the tree in a soft substrate in Iriomote Island, Japan (left). These extensive winding buttresses are probably a response to heavy winds and annual typhoons. The extensive sinuous buttress roots of *Xylocarpus granatum* (right) are clearly exposed on an eroding bank.

Adaptation to Anaerobic Conditions

Lenticels

These are pores, equivalent to stomata in the leaves, which occur on the trunks and exposed roots. Their function is to allow gas exchange. Large lenticels look like small eyes, hence *Bruguiera hainesii* which has numerous of these large lenticels on its trunk, is known locally in Malaysia as 'mata buaya' or 'crocodile eyes'.



Bark of *Bruguiera hainesii* with lenticels which resemble 'crocodile eyes'. The Malay name for this rare and threatened species is 'mata buaya' (crocodile eyes).

Pneumatophores

These are breathing roots that stick up from shallow horizontal roots (called cable roots), out of the low-oxygen mud into the air or oxygenated water. Pneumatophores vary in shape and size for different species and in different environmental conditions. The pneumatophores of *Avicennia* are usually around 30 cm high whilst those of *Sonneratia* are thicker and higher. The pneumatophores have abundant lenticels which allow gas exchange (see above).

In addition, the pneumatophores (and also the part of the stilt roots in *Rhizophora* that penetrates the soil) are largely composed of aerenchyma – a spongy plant tissue with air spaces. The air spaces enable gas exchange to take place by diffusion with the underground roots (Hogarth, 1999).

Thus *Avicennia* has a cable root system which grows just below the soil surface and spreads out horizontally. This cable root system helps in anchoring the tree in the soft substrate. Then there are the pneumatophores which grow up from these cable roots and allow gas exchange. Finally, there are roots which grow into the substrate and absorb nutrients.

The pneumatophores of *Bruguiera* are known as knee roots because they grow out of the mud from cable roots and bend back down like a knee, going back into the mud and then out and back again.



Pneumatophores radiating out from the main trunk of *Sonneratia alba* via cable roots (not visible: just under the soil surface).



Slender aerial pneumatophores of *Avicennia* grow vertically upwards into the air (left). Exposed (eroded) substrate shows horizontal cable roots of *Avicennia marina* that spread radially from the parent tree with pneumatophores growing vertically up and nutrition roots growing down (right).



The aerial roots of *Bruguiera gymnorhiza* grow out from the horizontal cable roots and then back again, resembling knees, thus the common name of 'knee root'. These knee roots function as breathing roots. The reason these knee roots are so prominent here may be because they are sediment starved.



The peg roots (pneumatophores) of *Xylocarpus moluccensis* at Palian, Trang, Thailand.

Animal Adaptations

Like plants, animals also need to adapt to survive in the harsh intertidal environment. Perhaps one group of animals that adapted remarkably well in this intertidal system are the mudskippers. These fish have become amphibious (being able to survive in and out of water).

Readers can refer to Ng et al. (2008) for more details on this topic of animal adaptations.



A pair of amphibious giant mudskipper (*Periophthalmodon schlossteri*) seen excavating at the entrance of their burrow (left). The fish on the right has just spat a lump of mud to the edge of its burrow (the splash is visible) so maybe these fish should be renamed as 'mud spitters'? Two giant mudskippers seen in a courtship ritual next to their flooded burrows (right). These fish spend a lot of time maintaining their elaborate burrows that trap air underwater, and where the eggs are laid and hatched. For further reading, please refer to Ishimatsu et al. (1998, 2007).

Avoidance

Most of the animals living in or just above the ground are marine animals so, unlike the vascular plants (discussed above) which are of terrestrial origin, these animals have to adapt to a low-salt environment (especially in rains during periods of exposure). Of course, many animals have the advantage over plants that they are mobile (although some of the bivalve molluscs are virtually sessile and even the gastropod molluscs have limited mobility) and are able to move to less hostile habitats.

The sesarmid crab *Episesarma versicolor* climbs up stilt roots and tree trunks (thus avoiding the change in water levels) with flooding tides rather than stay in burrows in the mud, like most other mangrove crabs.



Some sesarmid crabs, like this *Episesarma versicolor*, avoid rising tidal waters by climbing up roots and trunks (top). Mud funnels, probably built by some sesarmid crabs, prevent or reduce inundation by tides (bottom). Other crabs (e.g. fiddler crabs) just plug up the top of their burrows with tight-fitting mud caps, when the tide comes in.



The grooved and fine setae covered plate helps aerate (add oxygen) to water held in the gill chambers of this crab. This allows the crab to extend its stay out of water.

Adaptation to desiccation

Littoral animals have also to be able to withstand exposure or have adaptations that prevent desiccation (dehydration) during exposure. It is thus not surprising that the ground-living animals of mangroves are crustaceans and molluscs (that have shells to prevent desiccation). Also, many animals have adapted to living outside the aquatic milieu for short periods of time by having mechanisms to wet their gills (as seen in the sesarmid crabs as well as in mudskippers). The drier environment has also forced many of the molluscs to adapt their sexual apparatus as well as behaviour to living in a more terrestrial environment.

Adaptation to anaerobic conditions

Like their plant counterparts, animals that live in the mud must adapt to anaerobic conditions. Many of these animals have also adapted to being able to breathe on land. Another prominent group (that lives in the substrate) is the worms (like the blood worm *Glycera*) that have the necessary blood pigments with high oxygen-capturing capacity. Whilst the roots of plants are able to modify their rhizosphere, burrowing animals e.g. crabs and the mud-lobster (*Thalassina anomala*), as well as the mudskipper (*Periopthalmodon* spp.) can significantly modify the soil environment by oxidising the soil around and in burrows as well as in the substantial mounds thrown up in the burrowing process, as by the mud-lobster.



Mudskippers, like the gold-spotted mudskipper (*Periophthalmus chrysospilos*), are amphibious fish that are able to stay out of water for a period of time. They still have gills but have become air-breathing. This one is hanging onto a mangrove pneumatophore (breathing root for both the plant and the fish!) with the rising tide.

Opportunistic detritivory

There are few herbivores in the intertidal environment (however, leaf-eating monkeys when present can contribute significantly to herbivory as does the very episodic insect plague), mainly because of the xeromorphic leaves. The presence of high tannin content in mangroves is also believed to be the reason for the reduced herbivory. A number of species of crabs, however, have been able to take advantage of the high leaf litter fall of mangroves by utilising this abundant source of detritus. The mangrove ecosystem is predominantly detrital-based so that some of the key detritivores may be considered keystone species of these ecosystems.

Arched bridges can be constructed with properly stacked bricks. If a single brick is removed, most of the time the arch remains intact. However, there is a single brick, which if removed, will cause the whole structure to collapse. This is the keystone brick. So, a keystone species is a species, if removed, will cause the whole ecosystem to collapse. In the mangroves, Smith III et al. (1991) considered burrowing crabs to be keystone species for their role in nutrient recycling.



These mangrove sesarmid crabs feed on fallen mangrove leaves and other mangrove litter and form the basis of the detritivore link in the ecosystem. Some believe them to be a keystone species in the mangrove ecosystem. These crabs are edible (foreground), and are a key ingredient in Thai mango salads (background). If this indeed turns out to be a keystone species, then there should be controlled harvesting of this species.



Chapter 3

ECOSYSTEM FUNCTION

An ecosystem consists of many organisms which have specific functional roles. This is very clear when we look at the food chain which consists of various hierarchical levels (called trophic levels) each of which comprises organisms with the same functional role. The producers are the only organisms that can utilise energy (usually energy from the sun but some of them are able to utilise chemical energy, as in the case of sulphur-reducing bacteria) to synthesise organic carbon. All the other organisms in the ecosystem are dependent on this organic carbon. Consumers are organisms that feed on the producers (or other consumers). The laws of thermodynamics apply in this trophic conversion in that energy is lost when it flows from producers to consumers and lost again when it flows from one consumer to another. This is why there usually are only two or three levels of consumers and why there must be many more producers than consumers and more primary consumers (herbivores) than secondary consumers (carnivores), with the number of top predators being very low. This explains the food pyramid that is often used to show the numbers of organisms in various hierarchical classes in an ecosystem. Another group, the decomposers, are organisms that obtain their energy by breaking down dead organisms. Fungi and bacteria form the main decomposers in many ecosystems. In the mangrove ecosystem, crabs and termites are major decomposers in that they feed on dead leaves (or detritus, which is why these crabs are also known as detritivores). The producers, consumers and decomposers form an intricate relationship, and live in dynamic balance to maintain a healthy, functional ecosystem.

3.1 PRODUCERS

Primary Production by Vascular Plants

The main primary producers in the mangroves are vascular plants - the trees and shrubs. Gross primary production is the total energy fixed by plants during the process of photosynthesis. The plant itself uses part of this energy for metabolic processes; what remains is converted to plant biomass, which then becomes potentially available to other organisms (herbivores and decomposers). This constitutes the net primary production and essentially consists of the growth in biomass as well as losses (from the plant) in terms of litter production (both above- and below-ground) and root exudates. Fig. 3.1 summarises the different components of primary production.

Primary Productivity

Gross Primary Productivity (GPP) = all the carbon fixed during photosynthesis

(Net Photosynthesis = photosynthesis and respiration during photosynthesis)

Net Primary Productivity (NPP) = GPP – respiration

NPP = Biomass increment + litterfall (+ herbivory)

Fig. 3.1 The different components of primary productivity. Gross primary productivity (GPP) is measured by gas exchange meters but during the day, the gas exchange meters measure photosynthesis and respiration at the same time. This is referred to as net photosynthesis.
Gross Primary Production

Gross primary production of mangrove trees is estimated by gas exchange methods using portable photosynthesis meters to do the measurements and scaffolding tree towers to allow measurements to be made at different heights of the tree canopy. The rate of gross primary production varies through the day depending on various environmental factors like light and temperature. In a 20-year-old *Rhizophora apiculata* forest stand in Malaysia, Gong et al. (1992) found that the rate of net photosynthesis varied between 11.0 and 5.6 micromoles of carbon per square metre of leaf per second (µmol C m⁻²s⁻¹) from the top of the canopy to the bottom of the canopy due to the different light levels. The rate of net photosynthesis also varied in mangrove stands of different ages but part of the difference could be due to environmental factors like salinity. Respiratory losses can be quite high in mangrove ecosystems because considerable respiratory energy is necessary for salt exclusion and excretion.

Net Primary Production

The standing plant biomass is the biomass present in an ecosystem at any one time. Aboveground biomass in mangroves can be as high as 460 t ha⁻¹, found in an old *Rhizophora apiculata* dominated forest in Malaysia (Putz & Chan, 1986) or as low as 7.9 t ha⁻¹, found in a *Rhizophora mangle* stand in Florida (Lugo & Snedaker, 1974). Root biomass, including belowground roots, pneumatophores and prop roots can form a substantial portion of the total mangrove stand (Komiyama et al., 2008). Based on data obtained from 12 mangrove stands, Komiyama et al. (2008) estimated the ratio of above-ground biomass to below-ground biomass (T/R) in mangroves to be generally between 2 and 3; whereas the T/R ratios in upland forests (Cairns et al., 1997) were between 4 and 4.5. Thus mangroves have a relatively larger amount of root biomass compared to upland forests, probably due to the need to support mangrove trees growing in the soft substrate.

The net primary production is the sum of the increase in standing biomass plus the aboveground (leaves, twigs, flowers, fruit, etc.) litter production, plus the below-ground or root litter production, plus the root exudates production, plus losses through herbivory.

Plant biomass increment

The biomass the plant puts on in a year is part of the net primary production. In the mangrove forest, the annual increment in above-ground biomass ranges from 4 t ha⁻¹ yr⁻¹ in an *Avicennia* mangrove forest in Mexico (Day et al., 1996) to 26.7 t ha⁻¹ yr⁻¹ in a *Rhizophora* forest in Thailand (Christensen, 1978).

Very little has been done on below-ground biomass increment in mangrove ecosystems. Considering that the below-ground root biomass could be up to 57% of the biomass as in the case of *Bruguiera exaristata* (Comley & McGuinness, 2005), it is possible that the below-ground biomass increment could be a significant contributor to the total biomass increment. Ong et al. (1995) estimated below-ground root productivity of a *Rhizophora apiculata* stand to be 0.42 t ha⁻¹ yr⁻¹. In the same stand, the canopy (leaves and branches) productivity was 0.52 t ha⁻¹ yr⁻¹. Thus, the below-ground productivity is almost as high as the productivity of the canopy although the below-ground biomass is only about half that of the canopy in this mangrove stand (Fig. 3.2).



light, temperature and relative humidity). The twin-tower construction is a safety feature to add stability to the structure.



Fig. 3.2 Partitioning of the biomass and the growth of a 20-year-old Rhizophora apiculata stand in Malaysia. For more details, please refer to Ong et al. (1995).

Box 3.1 Estimating the Biomass of a Tree

A useful way of estimating the biomass of a tree is through allometry. The relative growth of one part of a plant (or an animal) is usually proportional to that of another part of the plant. The relationship between the two variables can be expressed by the generalised allometric equation:

 $y = bx^k$

where x is the independent variable, y is the dependent variable, and b and k are the allometric constants. The equation is often represented by logarithmic coordinates as a linear regression:

 $\log y = k \log x + b$

with *k* forming the slope of the equation and *b* the intercept.

In the case of estimating the biomass of a tree (y), a parameter that is easy to measure like the girth or diameter of the tree measured at breast height (1.30 m) is used as x. Thus, the regression equation becomes:

Log biomass = $k \log \text{GBH}$ (girth at breast height; or DBH – diameter at breast height) + b

The biomass can be total biomass, above-ground biomass, trunk biomass, root biomass etc.

The example here from Ong et al. (2004) illustrates how these allometric regressions are obtained. Trees of a species (in this case *Rhizophora apiculata*) covering the entire range of GBH (3.5–77 cm) are selected. The GBH is measured for each tree before it is felled. Each felled tree is then divided into the various components including the trunk, branches, twigs, leaves, reproductive parts and stilt roots, and every one of these components is then weighed in the field. After the above-ground components have been removed, the stump of each stilt root is followed down to its tip or as far as possible (down to at least 1 m depth) by loosening the soil around the root with jets of water generated by battery-powered submersible bilge pumps. These roots constitute the below-ground component. The extraction of underground roots is not easy (see photos below) and extremely labour intensive (taking about 30 man-days just to extract the root of a medium-sized tree) so not many allometric regressions have been established for the underground roots of mangrove trees (e.g. Bouillon et al., 2008).



Extracting the underground roots of a *Rhizophora apiculata* tree. Using bilge pumps to loosen the soils in order to free the roots (left) and still following the roots with bare hands despite the tides having come in, to ensure minimal loss of roots (right).

Samples of every component are weighed in the field and then taken back to the laboratory for drying at 105°C to constant weight, to obtain wet to dry weight conversions. The total dry weights of each of the components of every tree are then tabulated against its GBH. This was done for all 18 trees for the different components, and also for the total above-ground biomass as well as the total below-ground biomass and finally, the total biomass of the tree. The regressions of the various biomass components against the GBH, after logarithmic conversion, are then plotted and the equations obtained.

Examples of the allometric regressions obtained by Ong et al. (2004):

 $Log biomass_{total} = 2.253 logGBH - 1.943$

 $Log biomass_{below-ground} = 2.611 logGBH - 3.454$

Once the allometric regression equations have been calculated, the biomass of any tree of that species can be obtained by measuring just the GBH of the tree. If the GBH of all the trees in a plot is measured, the biomass of the plot can be estimated. If the biomass is estimated at two (or more) different times, it is possible to estimate the biomass increment and the rate of growth.

Examples of allometric regression equations for mangrove trees (different species and different plant components) can be found in various publications including Clough (1992), Ong et al. (2004), Comley & McGuinness (2005), Bouillon et al. (2008), and Komiyama et al. (2008).

Litter production

Small litter (flowers, leaves, twigs and small branches) production in the mangroves ranges from 4–13 t ha⁻¹ yr⁻¹ (Bouillon et al., 2008). These rates vary with latitude, with the highest values (average of 10.4 t ha⁻¹ yr⁻¹) between 0 and 10° latitude and the lowest values (average of 4.7 t ha⁻¹ yr⁻¹) at latitudes $> 30^{\circ}$.

Fine roots are also lost as litter underground. It is difficult to estimate fine root litter production in the mangrove vegetation but the amount can be considerable. The other component lost from roots is soluble root exudates. This is soluble organic matter that leaches out of living roots into the soil. Again, this is difficult to measure accurately and may also be a significant production.

As can be seen from the above discussion, we lack information on the below-ground component of productivity and more studies are needed to address this.

Primary Production of Algae

The mangrove ecosystem comprises not only the terrestrial forest discussed above but also the aquatic component: the waterways. We need therefore to also look at primary production in the aquatic component. Algae are the primary producers in this case.

Algae are basically of three types: periphyton which grow on the surface of other plants (e.g. mangrove roots); benthic algae (often diatoms) which grow on the mud surface (usually on mudflats), and phytoplankton which live in the water column. The contribution of these components to the overall primary production of the ecosystem is highly variable from site to site, depending on factors like relative proportions of these various components and the vascular plants, as well as climatic variables like the light available to these organisms. In most riverine and estuarine mangroves, the primary production of the higher plants far exceeds that of the algae.

In Florida mangroves where shading is not severe, periphyton production on prop roots reached 0.14–1.1 grams of carbon per square metre per day (g C m⁻² d⁻¹), equivalent to 0.5–4 t C ha⁻¹ yr⁻¹ (Lugo et al., 1975; Hoffman & Dawes, 1980).

Kristensen et al. (1988) estimated the benthic algal production in a Thai mangrove forest to be 110–180 milligrams of carbon per square metre per day (mg C m⁻² d⁻¹). The production from the trees in this forest was 1,900–2,750 mg C m⁻² d⁻¹. Thus benthic production was less than 10% of the higher plant production.

In mangroves where very little light penetrates the water column because of the turbid waters, phytoplankton productivity is low. In such a forest in Malaysia, plankton gross primary productivity was found to be only 3.5 t ha⁻¹ yr⁻¹, with net primary productivity being practically nil (Ong et al., 1984).

3.2 CONSUMERS (HERBIVORES AND CARNIVORES)

This high net primary production in the mangroves supports the other trophic levels in the mangrove ecosystem through the grazing food chain and through the detrital food chain. In the grazing food chain, the living parts of the plants are eaten by herbivores (primary consumers) which use part of the energy consumed for their own metabolic processes. The energy that

remains is converted into biomass and this becomes available for carnivores (secondary consumers) when they eat the herbivores and these carnivores in turn, 'pass on' the energy to the next trophic level – other carnivores (tertiary consumers) which eat them. The detrital chain starts off with the dead materials (leaf litter, roots and woody tissues). Organisms like crabs consume this dead material and in turn, these detritivores are eaten by larger carnivores in the detrital food chain. The detrital food chain is the dominant one in many mangrove ecosystems.

The Grazing Food Chain

Studies (e.g. Robertson & Duke, 1987) have shown that herbivory may not be very significant in the mangrove ecosystem. For example, grazing on mangrove leaves by insects and arboreal crabs usually accounts for only a small percentage of the leaf production. The amount of grazing is very variable and depends on the species of tree, sites, and even between individual trees. A survey of 25 species of trees in Australian mangroves (Robertson & Duke, 1987) showed that direct grazing by herbivores accounted for losses of 0.3-35% of the total expanded leaf area. In the dominant *Rhizophora* forests in Australia, some 11 g m⁻² yr⁻¹ (or 2.1% of the canopy production) entered the grazing chain. However, it should be noted here that leaf-eating monkeys, which can be a significant consumer of mangrove leaves (e.g. Ong, 1995) are not found in Australasia. In the mangrove forests of Malaysia, three species of monkeys consume mangrove leaves. These are the long-tailed or crab-eating macaques (*Macaca fascicularis*), which also feed on crabs, as their name suggests; the silvered langur or silvered leaf monkey (*Trachypithecus cristatus*), and the proboscis monkey (*Nasalis larvatus* – found only on the island of Borneo). These monkeys (especially the latter two) can consume a large proportion of the leaves of a forest (sometimes selectively denuding one particular species) (Ong, 1995).

There is very little quantitative information on the next step of the mangrove food chain – the herbivore-carnivore link and on the carnivore-carnivore link following this. It appears likely that insectivorous birds and bats (in some of the mangroves) consume some of the insects that graze the leaves. Some of these birds could in turn be eaten by snakes (in some of the mangroves).

A major difference between terrestrial and aquatic ecosystems is that in terrestrial ecosystems, only about 10% of plant production enters the grazing chain; another fraction enters the decomposer chain, and the rest constitutes the standing biomass of the vegetation. In the aquatic ecosystems, however, the plant (phytoplankton) production is almost completely grazed and the remaining standing biomass may be low. This is true in the mangrove waterways where the phytoplankton is highly grazed by herbivores almost as soon as they are produced. This results in a situation where the standing biomass is low but the production (calculated on a yearly basis) can be high. However, plankton productivity in many mangrove waterways may be low because of the turbid waters.

The fish communities in the mangroves have been of much interest, especially since many of the species are of commercial importance. Examples include anchovy, sea bass, grouper, and snapper. Shrimps and other crustaceans are also found in the mangrove waterways. Many studies (e.g. Chong & Sasekumar, 1981; Rodelli et al., 1984) have elucidated the feeding habits of these organisms (partly to try to resolve the question of how important mangroves are to coastal fisheries). This is not a simple task as these organisms can vary from being herbivores in their planktonic stage, to becoming tertiary consumers when full-grown; and most organisms have more than one main source of food.

Box 3.2 Primate Herbivores of the Mangroves of Borneo

The grassland ecosystem has bisons (*Bison bison*), the sea grass ecosystem has dugongs (*Dugong dugon*) and the mangrove ecosystem has proboscis monkeys (*Nasalis larvatus*). These are not only iconic but also rare mammalian herbivores that play important functional roles in their respective ecosystems.

The mangroves in Borneo are home to a number of species of monkeys. The long-tailed macaque (*Macaca fascicularis*), which is also known as the crab-eating monkey, is the most common but the mangrove forest is only one of many tropical ecosystems where they can be found. On the other hand, the silvered langur (*Trachypithecus cristatus*) is usually restricted to the mangrove and its adjacent riverine ecosystems. The proboscis monkey is not only generally confined to the mangrove and adjacent peat-swamp forest ecosystems but is endemic to Borneo. The diet of leaf-eating monkeys (the proboscis monkeys also belong to this group) is confined almost entirely to leaves. To help them digest their high cellulose diet, they have long intestines and hence their characteristic big bellies. They are not fruit-eaters and a diet high in fruit sugars is not suitable for them. Herbivores are generally rare in mangroves, perhaps because mangrove leaf and bark contain rather unpalatable chemicals like tannins and other polyphenols, but both the silvered langur and the proboscis monkey have been able to adapt.

These monkeys tend to be very selective on the type of leaves they eat, usually the young leaves of particular mangrove species like *Sonneratia caseolaris*. They thus need large areas of forests to forage for their nutritional needs. Reducing their range could lead to dire consequences, like the degradation of the forests they live in, as reported by Ong (1995) of the silvered langur in Peninsular Malaysia.

The troop of the proboscis monkeys is a very hierarchical and organised social system. Each troop (usually with 10 to 20 members) is composed of a core family group led by a dominant (or alpha) male and his harem of half a dozen or more females and their juveniles. The other males form the peripheral group of the family. Males from this outer group will compete to replace the alpha-male. As a result of his dominance, the alpha- male is morphologically different from the other males. Not only is the alpha-male bigger in size but he also has a much bigger nose (the proboscis, after which they are named) and a distinctly different coat. This distinguishing feature is probably caused by a behavioural-endocrinological interaction.

Perhaps, mainly as a result of a number of television documentaries shown worldwide, the proboscis monkey has become an icon for the mangrove ecotourism industry in Borneo. The continued destruction mangroves and peat-swamp forests is now posing a great threat to these rare primates. One of the biggest threats is from the burgeoning palm oil industry's hunger for land suitable for plantations. The island of Borneo (with the Indonesian province of Kalimantan and the Malaysian states of Sabah and Sarawak) has become prime target. The mangrove and peat-swamp ecosystems, being both under-valued and suitable for conversion to oil palm plantations are bearing the brunt of this large-scale assault. The huge expansion of the oil palm industry is the result of increasing demand (and hence the increase in price and profitability) for this edible oil. Apart from the increase in demand, the recent switch from growing grain (particularly corn or maize) for food to grain for fuel (i.e. bio-fuel) has resulted in the lower production of edible oils. This, together with the increase in the price of mineral oil was the reason for the recent alarmingly huge jump in world food prices, leading to an even hungrier world.

The switch of crops for food to crops for fuel is essentially the unwitting result of one of the mitigation measures of the Clean Development Mechanism (CDM) of the Kyoto Protocol. Whilst the use of renewable bio-fuels may superficially look like a good CDM mitigation measure, the longer-term downstream impact seemed not to have been considered by the proponents of this policy. One adverse impact is the loss of biodiversity (as a result of converting mangrove and peat-swamp forests to oil palm plantations) and the further threat of extinction to already threatened primates like the proboscis monkeys.



An alpha-male proboscis monkey (*Nasalis larvatus*) is highly sex hormone-charged, and is morphologically and physiologically very different from the non-dominant males of the troop. The 'beer-belly' (from having a long gut) is typical of leaf-eating monkeys.



The silvered langur or silvered leaf monkey (*Trachypithecus cristatus*) (top left) consumes large quantities of mangrove leaves so that small areas of mangroves cannot support this species. The proboscis monkey (*Nasalis larvatus*) (top right) is found only in the island of Borneo. The crab-eating or long-tailed macaque (*Macaca fascicularis*) (bottom) is one of the most common monkeys in Malaysia that often reaches pest proportions. The mangrove is only one of the many habitats they inhabit. Unlike the silvered langur and proboscis monkeys (which are almost exclusively leaf-eating), this species is an omnivore, so leaves form only part of their diet.

Decomposers

Mangroves differ from terrestrial ecosystems in that *in situ* production by plants is not the only major carbon and energy source. In addition to material produced in the system itself, material carried in includes algae and sea grasses from the seaward side and litter from terrestrial vegetation (leaves and branches brought downstream from the catchment). These can contribute significantly to the decomposition food chain in some of the mangrove systems.

Another question arises with respect to decomposition in mangroves. Is most of the dead material washed out of the system prior to decomposition or does most of the processing occur *in situ?* This varies depending on various factors, with the tidal regime as one of the main factors, and the presence of detritivores and saprophytic organisms as another important factor.

Decomposition consists of three processes: fragmentation, leaching and saprophytic activity. All three are important in mangrove ecosystems though their relative importance depends on various factors such as the tidal regime and the presence of macro-consumers like crabs.

Fragmentation

Fragmentation of dead material in the mangroves is due to the action of physical factors like tides, winds and temperature as well as to structural weakening caused by chemical action and by the activities of animals (consumers like crabs). This fragmentation results in smaller particles, which are more readily available to microorganisms, as they now have a larger surface area relative to mass.

Leaching

In the mangrove ecosystem, leaching is obviously an important process because the dead matter (leaf litter, wood and roots) is in direct contact with water. According to Cundell et al. (1979), approximately 30–50% of the organic matter in the leaves is leachable, and the remaining fraction, which consists of plant structural material, breaks down more slowly. In most mangrove litter, close to 100% of mass and carbon loss is due to leaching of dissolved organic matter (DOM) (e.g. Robertson et al., 1992). This constitutes a source of food for organisms living in the water column. Another effect is the leaching of soluble tannin from leaf litter, making it more palatable and therefore helps in further decomposition.

Saprophytic activity

Saprophytes are organisms that feed by absorbing dead plant materials. In most terrestrial ecosystems, bacteria and fungi are the major decomposers. Some scientists consider them to be true detritivores since they feed on dead material (detritus). Yet other scientists prefer to differentiate them from true detritivores as they say that detritivores feed directly on dead organic matter whereas decomposers (including fungi and bacteria) excrete enzymes which digest the organic matter externally before they absorb the relevant nutrients. In the mangroves, many of the animals often considered detritivores (many types of crabs, gastropods and some shrimps) in reality do not feed on detritus directly, but on the assemblage of organisms that feed on the detritivores, including protozoans, nematodes and meiofauna and even macrofauna. Other organisms (like the leaf-consuming sesarmid and grapsid crabs), however, are also true detritivores as they feed directly on dead plant material.

Detritus is a relatively poor source of food for the microorganisms (bacteria and fungi), so they assimilate dissolved minerals in the surrounding medium to supplement the essential nutrients they obtain from the detritus. This is a very important function, as the low-protein detritus is converted to a high-protein microbial biomass that is then available for other organisms.



Bracket fungus (*Fomes* sp.) and termites (in frass tubes) are already decomposing the tree trunk even when the tree is still standing (left). Bracket fungus (*Ganoderma applanatum*) found in the mangroves (right). This fungus is also a pathogen on live sapwood, particularly of older trees.

The Detrital Food Chain

The detrital food chain is important in mangrove ecosystems. One way of determining if an organism feeds on detritus is to study its gut content. This could result, however, in a false conclusion if the dead material has been merely taken in and is not utilised but excreted. Another way of determining if an organism is a detritivore is to use carbon, nitrogen or sulphur stable isotope ratios. Different organisms have different ratios so if the organism has a ratio that is the same as (or close to) the ratio found in detritus, then, it is reasonable to conclude that the organism feeds on detritus.

Various studies have shown that many macrofauna in mangroves feed on detritus (e.g. Chong & Sasekumar, 1981; Rodelli et al., 1984). Of particular importance are leaf-consuming sesarmid and grapsid crabs. These have carbon isotopic ratios close to that of mangrove detritus, indicating that mangrove detritus is the major food source. These crabs can eat vast amounts of litter. Data summarised in Robertson et al. (1992) showed that litter consumption by crabs in tropical Queensland ranged from 28–71% of the litterfall. This explains why in some mangrove areas, the forest floor appears completely clean of leaves as the crabs have consumed or buried most of the leaves!

Studies looking at gut content (Chong & Sasekumar, 1981) as well as isotope ratios (e.g. Rodelli et al., 1984; Chong et al., 2001) have shown that the post-larvae and juveniles of various prawn species (e.g. *Penaeus merguiensis* in Malaysia) that inhabit mangrove forests and waterways also feed on mangrove detrital material including the organic aggregates formed from DOM leached out of mangrove detritus. However, the importance of mangrove detritus decreases



as prawns move offshore to join adult populations. For example, Chong et al. (2001) found in the Matang mangrove in Malaysia, that the contribution of mangroves to prawn tissues could be as high as 84% in the mangrove waterways, decreasing to 15–25%, just 2 km from the mangrove, to almost nil, 7-10 km offshore.

Carnivorous fish in the mangroves that feed on the prawn *Penaeus merguiensis* includes the barramundi (*Lates calcarifer*). Others like the mangrove jack (*Lutjanus argentimaculatus*) feed on leaf-consuming sesarmid crabs. In Malaysian mangroves, most of the carnivorous fish that come into the mangrove forests during high tide feed on leaf-consuming grapsid crabs. Thus, there is a clear link between detritus, detritivores and carnivores.

Export and Burial

Not all the production in mangrove ecosystems is used *in situ*. A proportion (sizeable in some areas) of the production is exported to the nearby waters (e.g. Gong & Ong, 1990; Alongi et al., 1998). This is one reason why mangroves are often said to be of great importance to the coastal region, as the detrital-based food chains are said to support near shore secondary production. More recent work using carbon isotope ratios in producers and consumers, however, have indicated that whilst mangroves do play such a role, their importance may vary from site to site (e.g. Chong et al., 2001).

There is another portion of mangrove production, consisting largely of mangrove roots and also part of the above-ground production that are neither used nor exported. This is buried in the mangrove sediments and is preserved under anaerobic or almost anaerobic conditions. Mangrove forests in the Indo-Pacific region store an average of 1,023 t C ha⁻¹, with 49–98% of this stored in the soil (Donato et al., 2011). This is much higher than the average storage of just over 200 t C ha⁻¹ in tropical terrestrial forests, with around 55% storage in the soil. This carbon sequestration function of the mangrove ecosystem is of particular interest currently in view of rising atmospheric carbon dioxide levels and climate change issues.

Chapter 4

SOCIO-ECONOMIC AND MANAGEMENT CONSIDERATIONS

4.1 MANGROVE GOODS AND SERVICES

Mangrove ecosystems not only produce goods but they also provide services. Not all are exactly the same, so it is important to realise that different mangrove ecosystems provide different goods and services (Ewel et al., 1998). For example, fast-growing mangroves (located in the ever-wet tropics) can sustainably produce timber, but not the slow-growing ones (usually located in the higher latitudes and with limited rainfall).

Mangrove Goods

Goods are products that have tangible values and that can be marketed. It is thus possible (without too many contentions) to put a value on these goods.

Timber

Timber is the most obvious mangrove forest product that has a tangible value and that can be (and is often) marketed. Many mangroves (particularly in former British colonies) are managed for timber production. Mangrove timber has many uses and has traditionally been used as firewood as well as being converted to top quality charcoal. Some mangroves trees (e.g. *Xylocarpus* and *Heritiera*) yield very fine furniture-grade timber but these rarely occur in large enough stands to be commercially viable. Poles of *Rhizophora* and *Bruguiera* make excellent piling, and many of the houses (e.g. in Singapore) built during the late 19th Century on such piles still stand today. Mangrove timber lasts a long time when it is buried in the ground, but breaks down rather rapidly if exposed.

Mangrove timber is also chipped and used for the manufacture of rayon. These are large-scale operations where extensive areas (tens of thousands of hectares) of some of the world's best *Rhizophora* forests have been harvested on a one-off basis. It is tragic that the mangrove woodchip industry (essentially controlled by a Japanese monopoly) has not taken greater pains to ensure sustainable harvests, given that the technology already exists.

Other forest products

There are numerous other local uses of mangrove forest products, from fishing stakes using the palm *Oncosperma tigillarium* to sugar, roof thatching and tobacco wrapper from another palm *Nypa fruticans*, and traditional medicines from almost every species of mangroves. [Please see the companion volume to this book on case studies of useful products from mangrove and other coastal plants by Baba et al. (2013)]. Various shellfish are collected on a subsistence level but crabs and shrimps collected from mangrove waterways are commonly traded internationally.

Fish

Mangrove waterways are rich fishing grounds and many commercial species can be found (Table 4.1). The traditional mangrove fisheries range from the mud crabs (*Scylla* spp.) caught by crab traps to high quality white prawns (*Penaeus merguiensis*) and pomfrets (*Pampus*



Mangrove timber of *Rhizophora apiculata* makes excellent charcoal (top row). Poles for piling are a timber product of the mangroves (bottom).



The young leaves of the mangrove palm, *Nypa fruticans* are used as wrappers of tobacco to make local cigarettes. Picture (left) taken in Trang, Thailand, shows the processing of the leaves into wrappers. The palm, *Oncosperma tigillarium* grows in clusters at the landward side of mangroves (right). Its poles are used as fishing and docking stakes.



Mud crabs, like the orange *Scylla olivacea* (left) and the green *Scylla paramamosain* (right), are caught using crab traps in the mangrove waterways or hooked out of their burrows in the mangroves.

Table 4.1 Checklist of fish and prawns from the Matang and Merbok mangroves (Khoo, 1989)

Fish

Ambassis gymnocephalus Ambassis kopsii Anodontostoma chacunda Apogon thermalis Arius caelatus Arius maculatus Arius microcephalys Arius sagor Arius spp. Arius venosus Boleophthalmus boddash Butis butis Caranx sexfasciatus Caranx speciosus Chorinemus Iysan Dorosoma nasus Eleutheronema tetradactylus Epinephalus sp. Epinephalus tauvina Eugnathogobius microps Eupleurogrammus intermedius Gerres punctatus Gymnura sp. Halophryne sp. A Halophryne sp. B Hamirhampus xanthropterus Johnius carutta Johnius goldmani Johnius sinaJohnius solado Ketengas typus Kowala sp.

Lagocephalidae Lates calcarifer Leiognathus brevivostris Leiognathus equulusLiza subviridis Liza vaigensis Lobotes surinamensis Lutjanus argentimaculatus Lutjanus monostigma Megalops cyprinoides Monodactylus argenteus Mugil spp. Muraenesox cinereus Mystus gulio Opistoptherus tardoore Osteogeniosus militaris Oxyurichthys microlipis Pampus chinensis Paraplotosus anguillaris Pellona elongata Pellona pelagicus Periophthalmodon schlosseri Periophthalmus koelreuteri Platycephalus crocodilus Pomadasys hasta Pseudorhombus arsius Pseudorhombus sp. Rastrelliger sp. Sardinella fimbriata Scatophagus argus Sciaena russeli Sciaena sp. Secutor ruconius Selar kalla

Setipinna taty Siganus javus Sillago sihama Sphyraena jello Stolephorus andhraensis Stolephorus heterolobus Stolephorus indicus Terapon jerbua Tetraodan fluviatilis Thrissocles dussumieri Thrissocles hamiltonii Thrissocles mystax Toxotes chatareus Toxotes jaculator Triacanthidae Trichiurus glossodon Trypauchenidae Tylosurus strongylura Upeneus sulphureus Valamugil cunnesius Valamugil seheli

Prawns

Acetes spp. Alpheidae Macrobrachium rosenbergii Metapenaeus brevicornis Metapenaeus dobsoni Metapenaeus ensis Metapenaeus lysianassa Parapeneopsis sculptilis Penaeus merguiensis Penaeus monodon *chinensis*) caught in bag nets to the tiny but seasonally abundant planktonic shrimps (*Acetes* spp.) caught in push nets. The revenue derived from fisheries far exceeds that derived from forestry.

Natural cockles

The blood cockle (*Anadara granosa*) grows naturally in some mudflats adjacent to mangrove areas. Some of these mudflats have these cockles all the time whilst others have cockles growing only intermittently. These are natural cockle beds. Other mudflats do not naturally have cockles but cockles will grow, if seeded. Natural cockle beds are thus a most valuable asset in this multimillion-dollar industry. The destruction of adjacent mangroves as well as any interference with the normal pattern of water circulation (which allows the cockle larvae or spat to settle) could easily destroy natural cockle beds. Destruction of mangroves adjacent to cockle beds could also have adverse effects (e.g. slower growth) on the cockles.

Floating cage aquaculture

There are floating aquaculture cages in many mangroves. These are used mainly for the culture of fish like seabass (*Lates calcarifer*), snapper (*Lutjanus* spp.) and grouper (*Epinephalus* spp.), and shellfish like oysters (*Crassostrea* spp.) and mussels (*Perna viridis*). This aquaculture practice has been shown to be sustainable as well as having minimal impact (especially if the estuary is well flushed) on the estuary and the adjacent mangrove ecosystem.



The blood cockle, Anadara granosa, grows naturally or is seeded on mangrove mudflats.



Mangrove Services

Mangroves provide many services but these are less tangible than goods and although there have been numerous attempts at valuing these services, these values always remain contentious. Since such services have no market value, their values are ignored by the present economic system. The many services of mangroves include:

Maintenance of channel depth

The presence of mangrove vegetation causes an asymmetry in tidal currents. The ebb current is faster than the flood current in creeks with vegetation (drag is caused by mangroves). The faster ebb current scours out the mangrove channels thus reducing siltation in mangrove channels (Wolanski et al., 1992; Furukawa & Wolanski, 1996). If the mangrove vegetation is removed (as when shrimp ponds are constructed in mangroves), the tidal asymmetry and scouring effect are reduced. These channels with symmetrical tidal currents will become more susceptible to silting. Such silting will prevent the free navigation of rivers and create problems for fishers.

Sediment accretion and coastal protection

Sheltered coasts allow sediments to accumulate and it usually does not take long for mangrove vegetation to start growing. These plants then consolidate the sediments with their roots as well as cause hydrodynamic changes that then actively trap more sediments. The above-ground roots and stems of mangroves slow down the water coming in with the flood tide and, in the process, sediments are deposited. So, mangroves actively aid in the accretion of sediments that leads to increase in coastal land area. This is the natural process of coastal reclamation with no cost and with positive environmental impact. This process is however only applicable to accreting coasts.

Since mangroves occur in sheltered coastal areas, it seems a contradiction to say that mangroves offer protection against coastal erosion. The protection that mangroves offer is mainly during episodic adverse weather events (like hurricanes and cyclones). They reduce the severity of the effects of these storms. The mangroves of Sundarbans in Bangladesh and India considerably reduce the severity of tidal bores (caused by episodic severe storms and the even more occasional tsunamis) before they reach populated areas inland. Thus mangroves do offer protection from coastal erosion, especially during severe episodic storm events. A lack of mangrove vegetation will increase the severity of the damage.

Bird sanctuary/migratory stops

Mangroves, like all wetlands, are roosts for many birds unique to this environment. They also act as resting and feeding areas for migrating birds. Widespread destruction of mangroves could upset these roosting and migrating bird species. Thus, not destroying mangroves is part of being responsible international citizens.



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Mangroves and adjacent coastal fisheries

One of the most compelling reasons for the conservation of mangroves is their possible role in sustaining coastal fisheries. Mangroves and salt marshes allegedly 'outwell' carbon and nutrients to adjacent coastal environments, which nourish thriving shrimp fisheries. Quantifying the amount of outwelling is still proving elusive almost half a century after this concept was first introduced in 1968 by E. P. Odum (e.g. Nixon, 1980; Simpson et al., 1997).

The economic returns from fisheries within mangroves and in adjacent coastal areas are about an order of magnitude more than that from forestry products. How much mangroves actually contribute to adjacent fisheries is a very relevant but difficult question to answer. A number of studies have shown good statistical correlations between the area of mangroves and the amount of prawns landed. Though these correlations have not been clearly demonstrated to be causal, the evidence is convincing, although more direct and quantitative links have still to be



Bag-nets are commonly used in mangrove estuaries. These nets are usually deployed just before the spring high tides (the neap tide currents are usually not strong enough, in many places) and the strong ebbing tidal currents wash the fish into the nets. The nets seen above are not deployed.

established. Even if the mangroves provide adjacent coastal fisheries with only minimal nutrients, mangroves are still important breeding and nursery grounds. For this alone, there is every reason to conserve mangroves wherever possible: the precautionary principle certainly can be most appropriately applied here.

Sequestration of atmospheric carbon dioxide

The primary productivity of mangroves is amongst the highest of natural ecosystems. Often, a high proportion of the productivity is partitioned to the roots. Since the roots are in anaerobic conditions, much of the shed and dead roots are preserved underground (turning to peat). Part of the above-ground productivity is sometimes also buried, leading to even more sequestration of atmospheric carbon. Digging up mangrove soils (e.g. in the construction of aquaculture ponds) not only stops carbon fixing by the plants but also oxidises stored carbon into carbon dioxide. Conserving mangroves thus alleviates the problem of increasing atmospheric carbon dioxide.

Even animals – molluscs like cockles and oysters – store carbon in their substantial shells (as carbonates) and this contributes to the carbon sequestration process. The natural sequestration by cockles (as calcareous shell) has been estimated at 0.25 t C ha⁻¹ yr⁻¹ (Ong, 1993).

Developing countries that conserve their mangroves should be able to use this to offset carbon dioxide taxes. A more comprehensive treatment of mangrove carbon can be found in Ong (1993).

By and large, mangroves are highly productive ecosystems (see main text). Mangrove timber is used for a number of products: charcoal, fuel wood, piling and rayon (a fabric made from mangrove wood fibres). For fuel wood and charcoal use, the carbon is quickly returned to the atmosphere on burning. Mangrove piling can last for many tens of years (e.g. many old houses built in the early part of the last century sit on mangrove pilings). When converted to rayon, the fabric will last a good decade. So, for the above-ground harvested mangrove timber, the sequestration time could vary from months to a century or more.

When mangroves are harvested, only the above-ground biomass is removed. The roots however remain underground (in anoxic or almost anoxic conditions) and eventually become peat or

even coal. Here the sequestration could be for hundreds or thousands of years. So when carbon sequestration is considered, it is very important to understand the time scale involved.

If, on the other hand, mangrove land is dug up and converted to aquaculture ponds, some 75 t C ha⁻¹ y⁻¹ (over a 10-year period) is estimated to be released into the atmosphere (Ong, 1993), which is some 50 times the sequestration rate.

In summary, it is important not only to understand the time period carbon is sequestered when mangrove timber products are put to different uses; but also whether the ecosystem is used on a sustainable basis or put to alternative uses, like conversion to pond aquaculture (as in so many of the world's mangroves). Carbon credits have been given and sold but vital questions remain unanswered. Perhaps the various blue carbon projects will now be able consider these questions.

Box 4.1 CDM, REDD and Blue Carbon

Carbon trading was first initiated under the Kyoto Protocol where developing countries (Annex A signatories) could use rehabilitated forests (pristine forests are not eligible for carbon trading under the CDM) to trade in carbon with developed countries (Annex B signatories). This comes under an article of the Kyoto Protocol known as the Clean Development Mechanism (CDM).

There are however many forests in developing countries that are either pristine or not exploited but these forests are not eligible for carbon credits under the CDM. There is now (arising out of the 2007 Bali Action Plan) another mechanism available to trade carbon from some of these forests. This new mechanism, like CDM, is under the United Nations Framework Convention on Climate Change (UNFCCC) and is known as REDD (Reducing Emissions from Deforestation and Forest Degradation). This recognises the fact that not destroying or degrading pristine forests is just as important as rehabilitating deforested ones. The more recent REDD + includes 'the role of conservation, sustainable management of forests and enhancement of forest carbon stocks.'

Carbon, by most peoples' reckoning is either black (graphite) or colourless (diamond), so what is blue carbon? It is nothing more than a recent jargon for carbon that has been sequestrated by oceans (yes, oceans are blue), including coastal ecosystems like salt marshes, sea grasses and mangroves (see *Blue Carbon Initiative* at: www.unep.org/ecosystemmanagement/Portals/7/Documents/factsheets/BlueCarbonInitiativeFactSheet.pdf).

This blue carbon initiative is essentially based on the belief that saving high carbon- sequestrating coastal ecosystems like mangroves from further destruction will contribute significantly to reducing carbon emission. The blue carbon initiative is a follow up to the Kyoto Protocol's CDM and the UNFCCC's REDD. Another objective of the blue carbon initiative is to overcome some of the shortfalls of CDM and REDD.

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When mangroves are harvested, only the above-ground biomass is removed. The roots however remain underground (in anoxic or almost anoxic conditions) and eventually become peat or even coal. Here the sequestration could be for hundreds or thousands of years. So when carbon sequestration is considered, it is very important to understand the time scale involved.

If, on the other hand, mangrove land is dug up and converted to aquaculture ponds, some 75 t C ha⁻¹ y⁻¹ (over a 10-year period) is estimated to be released into the atmosphere (Ong, 1993), which is some 50 times the sequestration rate.

In summary, it is important not only to understand the time period carbon is sequestered when mangrove timber products are put to different uses; but also whether the ecosystem is used on a sustainable basis or put to alternative uses, like conversion to pond aquaculture (as in so many of the world's mangroves). Carbon credits have been given and sold but vital questions remain unanswered. Perhaps the various blue carbon projects will now be able consider these questions.

Ecotourism

The adaptations of mangroves to an intertidal environment have aroused human curiosity. Examples of such adaptations include the stilt roots of *Rhizophora*, the pneumatophores (breathing roots) of *Avicennia, Sonneratia* and *Xylocarpus*, the knee roots of *Bruguiera*, and the prominent propagules (the seeds germinate whilst still on the trees and grow into 'seedlings' before they fall to the ground) of the Rhizophoraceae. Some of the plants (e.g. *Avicennia*) also have salt glands on their leaves that excrete salt. Numerous birds and other animals are also rare and almost unique to the mangroves. These include the milky stork (*Mycteria cinerea*), the night heron (*Nycticorax nycticorax*), silvered langur (*Trachypithecus cristatus*), crabs like the fiddler crabs (e.g. *Uca rosea* and *U. annulipes*), the mud-lobster (*Thalassina anomala*), and mudskippers. It is thus possible for tourists to spend an entire day in the mangroves looking at and appreciating interesting animals and plants. Many mangroves are potentially suitable for ecotourism. It is, however, important that tour guides are given the necessary training so that they can pass on the right information.



In recent years, many mangrove forests have become accessible through board walks. The Matang mangrove in Malaysia, with its board walks (photo), informative signage, arboretum, nature education centre, chalets and charcoal village, has become a popular ecotourism destination.



The attractive flowers of mangrove plants such as the red and strongly scented flowers of *Lumnitzera littorea*, and the pink to red calyx lobes of *Bruguiera gymnorhiza* would attract naturalists visiting the mangroves.



The fiddler crabs are commonly seen on the mangrove substrate. Only the males have the enlarged pincer. This pink clawed one is a right-handed *Uca rosea* (top). The male *Uca annulipes* seen here (bottom) is found on sandier substrate.



Canoeing is one of the apparently benign ecotourism activities in the mangroves. These pictures are of a pristine mangrove in Iriomote Island, Japan.



Crested serpent eagles (*Spilornis cheela*) in Iriomote, Japan are tame enough, especially the young ones (lighter-coloured), for ecotourists to get really up close and personal.

Box 4.2 Kuala Gula Bird Sanctuary in Matang

The Kuala Gula bird sanctuary is situated at the northern end of the 40,000-hectare Matang mangrove on the Straits of Malacca coast of Peninsular Malaysia. The main attraction for the avian species is the presence of two freshwater lakes (Stork Lake I and Stork Lake II) within the mangroves itself). These freshwater lakes provide environmental conditions that attract both endemic as well as migratory birds.

Mycteria cinerea, the milky stork (for which the freshwater lakes are named after), breeds in the mangroves and is perhaps the star or iconic species of the Kuala Gula bird sanctuary. The milky stork is listed in Appendix 1 of CITES and is classified as vulnerable (VU) in the IUCN Red List (2007). The locals used to collect their eggs (they are now totally protected) and over the years, their population has fluctuated wildly but more recently, the numbers seem to have recovered. Perhaps it is the populations on the other side of the Straits of Malacca, i.e. Sumatra, Indonesia (where the highest numbers of milky storks occur), that prevents the Kuala Gula population from going extinct. These birds were common through much of Southeast Asia but are now thought to be extinct in Thailand and Vietnam.



A milky stork (*Mycteria cinerea*) in flight at the Kuala Gula bird sanctuary (left). These birds were close to extinction (due to collection of eggs, amongst others) but their population seems to be recovering now, with the mangrove being gazetted as a bird sanctuary and awareness campaigns by the local NGOs. A flock of milky storks, that has just taken to the air from one of the Stork Lakes (right).

Another stork that is more commonly seen in Kuala Gula is the lesser adjutant stork (*Leptoptilos javanicus*). This is an even larger bird than the milky stork and is very often seen feeding on the mangrove mudflats or sometimes flying around. These are residents and thus can be seen all year round. Other birds that are commonly seen are a few species of egrets, herons and kingfishers. Almost 200 species of birds (both residents and migrants) have been reported, about half of them water

birds (see: www.wildasia.org). Raptors include the white-bellied sea eagle (*Haliaeetus leucogaster*), the osprey (*Pandion halietus*) and the Brahminy kite (*Haliastur indus*).

The Kuala Gula mangrove has become a popular site for bird watchers (both local and foreign). Wetlands International was responsible for initiating an educational programme to encourage the local population to look after the birds as well as involving the locals in ecotourism. The locals now offer conducted boat tours, and are also involved in mangrove protection and rehabilitation. This project has now been taken over by the Global Environmental Centre (a local NGO).



Raptors at the Kuala Gula bird sanctuary. Brahminy kites (*Haliastur indus*) with their reddishbrown plumage and contrasting white head and breast are commonly sighted (left and right). The greyish-brown individual at the far left is a juvenile.



A mangrove nursery established by local NGOs for mangrove rehabilitation in Kuala Gula.

4.2 VALUE OF MANGROVES

Mangroves provide many different goods and services that vary for different areas. The market value of mangrove goods is often limited and their services do not carry a market value. Often, even the goods are undervalued (usually due to rent seeking). So, in terms of value, mangroves are considered by economists as a market failure. When this happens, it is considered the role of governments to provide the necessary equity (e.g. Ong et al., 2001; Dodd & Ong, 2008). The governments of many developed countries (e.g. Australia, Japan and the USA) do this by protecting their mangroves very comprehensively through legislation and strict enforcement. Governments of less developed countries are often too impoverished to provide such or similar equity. Unfortunately, most of the world's mangroves occur in the developing countries and the consequence is that the world's mangroves are being rapidly destroyed or degraded (e.g. Spalding et al., 2010).

Monetary Value of Mangroves

It is extremely difficult to put an exact monetary value on mangroves. Different mangroves have different values. Essentially, one of the main reasons for the rapid loss of mangroves in many developing countries has been the extremely low value placed on these wetlands. Mangrove land should be considered of at least equal value to any other land with a sea frontage. In addition, there is the scarcity value as well as all the other ecological functions that it performs. It is easy enough to put a value on mangrove timber (although that used for woodchips, for example, may be undervalued due to monopoly or rent seeking), but the value of timber, although significant, is often much less than other products related to the mangroves, like fisheries. It must also be remembered that these are 'annual' revenues, since they can be harvested on a sustained yield basis. The less tangible values of mangroves are the non-use benefits – maintaining channel depth, prevention of erosion, carbon sink, etc. Thus mangroves should not be alienated as cheap land to be put to alternative use but must instead be considered rare and extremely valuable land to be jealously retained.

Sustainable Use Management

Mangrove forests have a good century of forest management history and some mangrove forests in South and Southeast Asia are considered to be well-managed for sustainable timber harvesting (making them the few tropical forests managed on a sustainable basis). The basic mangrove forest management system was designed by British foresters based on a simple rule of thumb, and modified over the years (Watson, 1928). This has turned out to be remarkably successful. One classic example is the Matang mangrove in Malaysia. Some issues encountered in the management of the Matang mangrove are discussed in the boxes below.

Box 4.3 Matang Mangrove Management

Recently, the Matang mangrove proudly achieved a century of forestry management. The original management was for the use of mangrove timber as fuel wood for locomotives that transported tin from mines inland around Taiping to Port Weld on the mangrove coast. The management system was based on rule of thumb, after keen observations by British foresters. Except for minor changes, the management system remains essentially the same to this day. Presently, it is based on a 30-year rotation with an annual coupe of 1,000 hectares with thinning (commercial as opposed to silvicultural) for poles at 15 and 20 years. Tree density is approximately halved at each thinning. Details of the system can be found in Ong (1982) and Chan (2001). There are also the classic of Watson (1928) and a number of Revisions of Forestry Working Plans: (Noakes, 1952; Dixon, 1959; Mohd. Darus, 1969; Haron, 1981; Gan, 1995; Azahar & Nik Mohd Shah, 2003), but these publications may not be as readily available.

Presently, the timber is used for poles (mainly as pilings) and the final fell timber is converted to charcoal (much of which is now exported to Japan and Korea, although there is still a local market for its use in specialised cooking).

There is no doubt that the Matang mangrove is a rare case of successful tropical forest management. The 40,000 hectares of mangroves have remained intact after a century of forest management. Our main task here is to discuss whether or not the Matang mangrove has been sustainably managed from not just the forestry but also the ecological as well as the economic aspects. We see these as useful 'lessons learnt' that may be applicable to the management of other mangroves.

Forestry production sustainability

Even though the forestry management system is based on simple rule of thumb, it has worked exceedingly well. After more than three harvest rotations, the Matang mangrove remains basically intact and credit must go to the Malaysian foresters who have taken the baton from the British foresters. There is no doubt that the system has been sustainably managed. Perhaps the more critical question is not just about sustainability but rather if maximum yield has been achieved. Related to this is whether the thinning regimes as well as the period of the harvest rotation are optimal; from not only the forestry production but also the ecological aspects.

Ecological sustainability

As a result of the preference for *Rhizophora* (mainly *R. apiculata*) in charcoal production, most (at least 30,000 hectares designated as production forests) of the Matang mangrove forest comprises the monoculture of this species. One of the obvious detrimental effects of the management system is the loss of species diversity. Whilst mono-specific stands is a natural feature of mangrove zonation, converting most of the mangroves to a monoculture of *R. apiculata* may not be a wise ecological practice. Matang is lucky in that only 30,000 hectares are used as production forests, with the remaining 10,000 hectares being left as protected or buffer zone. With a more holistic (especially now that the Forestry Department is now under the Ministry of Natural Resources where previously it was under the Primary Industries Ministry) and prudent practice, it is possible to improve the biodiversity of Matang forest by managing the protected or buffer area for maximum biodiversity.

One excellent practice in the Matang mangrove is the implementation of 'Working Plans' which are revisions of the previous management plan. There have been five of these plans since Noakes (1952); approximately one every decade. This allows a certain amount of monitoring of the forest (mainly on forest production) and provides the necessary

interventions. Unfortunately, there is no monitoring of the health of the forest on a more ecological and holistic basis. There is a need for a scientific unit, located within the Matang mangrove itself, to carry out this important task. This unit could work closely with researchers from the Forest Research Institute Malaysia (who used to have research plots projects in Matang) and from the universities (e.g. Universiti Sains Malaysia and Universiti Malaya).

Economic sustainability

Generally, as a result of low returns from mangrove goods, the value of mangrove is low and most mangroves are considered economic market failures. This means that governments have to provide equity. Thus in developed countries where mangroves occur (e.g. Australia, Japan and the USA) mangroves are given legal protection from degradation and destruction. Most of the world's mangroves are unfortunately located in developing countries and most of these governments (Thailand being a recent rare exception) cannot afford to protect their mangrove (see Ong *et al.*, 2001; Dodd & Ong, 2008).

The Matang mangrove is managed by the Perak State Forestry Department which provides the physical and human resource infrastructure and oversees the day to day management of the forest. Concessions are awarded to individuals to harvest poles or produce charcoal. Concessionaires are involved in the harvesting process and pay a premium to the forestry department. According to the latest available Working Plan (Azahar & Nik Mohd Shah, 2003), the revenue collected (some RM 1.3 million or USD 430,000) is slightly more than the running costs of managing the forest. The running costs, however, do not include emolument of forestry department staff or physical infrastructural costs (which may be close to half an order of magnitude more than the running costs). Despite a recent doubling of premium, the forestry department still provides a significant subsidy (we estimate this at a few thousand RM per hectare per year) to manage the system. The gate price of charcoal and poles from the Matang mangrove is worth only about RM 800 per hectare per year; which is a few thousand short of expenditure by the forestry department.

To put things into perspective, the returns from pole and charcoal production are only about a seventh of the revenues from fish landed in the area. The annual returns from a hectare of mangrove land used for shrimp aquaculture become even more staggering (some fifty times more) compared to its use for poles and charcoal. This is a major reason why much of the world's mangroves have been lost through conversion to aquaculture ponds. The bottom line is that the Matang mangrove management system is not economically sustainable and the likely reason is rent seeking (akin to monopoly).

Lessons learnt

First, there is no doubt that, by and large, the management of the Matang mangrove has been a great success; mainly in retaining the original 40,000 hectares for a century. The huge area available for management has been an advantage, especially with a quarter of the total area as protected or buffer zone. Nonetheless, it is far from perfect and improvements could include:

- Overcome the loss of biodiversity by planting a diversity of tree species in the protected and buffer area.
- Establish a Research Unit to monitor the health of the forest (including the re-establishment of research plots) as well as identify specific potential problems.
- Further increase the royalties for poles and charcoal so that forestry management can be run on an economically self-sustaining basis. Whilst this may not eliminate rent seeking, it will reduce it.
- Explore other means to ensure the economic and ecologic sustainability of the system.



In the Matang mangrove, the greater golden backed four-toed woodpecker (*Chrysocolaptes lucidus*) is a common sight in mature forest stands (especially those with dead trees). The one with the red cap is male and one with black and white cap is female. The mono-specific forest stands do not seem to have a deleterious effect on the bird fauna and many species of woodpeckers and other birds can be seen. Age of stands seems to matter more than the number of plant species. The presence of undergrowth also seems to favour avian diversity.



Manual harvesting (first thinning) in a 15-year-old stand of *Rhizophora apiculata* in Matang (left). The tree density is reduced to about half and a second thinning is carried out at 20 years. Each tree produces three poles. Poles are marked (for royalty collection) at collection stations before they are allowed to leave the mangroves (right). Poles are mainly used as pilings.



A beehive charcoal kiln in the final stage of a 'burn' and charcoal, the final product (inset). Most of the charcoal is now exported at a very low (economically unsustainable) price.



Final-felling area (30-year-old stand) where trees are felled, billeted and then wheeled (on the temporary plank track) for loading onto lighters and taken to the charcoal kilns. The timber is denser than seawater so cannot be floated out.

Box 4.4 Lightning Gaps in Mangroves?

These regular and circular (20–30 metres in diameter) gaps in the mangroves at Galley Reach, near Port Moresby in Papua New Guinea were first reported by Paijmans & Rollet (1977) and attributed to lightning strikes. In the Matang mangrove, these gaps are also visible from aerial photographs and have also been attributed to lightning strikes (Gan, 1995; Amir, 2012).

Our first experience with these gaps was during our study on leaf litter fall, in the late 1970s. On one occasion, a number of our leaf litter traps were filled with green leaves of *Rhizophora apiculata*. These traps were in or around one of these newly formed gaps. The gap was formed by complete loss of leaves over a very short span in time.



Gaps in a *Rhizophora apiculata* forest in the Matang mangrove, Malaysia. What appears to be the beginning of a new gap can be seen in the left foreground (yellowish-brown canopy) of this aerial photograph.

Our first thought was also, lightning, but we did not observe any burn or scorch marks. Paijmans & Rollet (1977) also reported (as did others subsequently working on these so-called lightning gaps) not seeing any evidence of scorch marks. The complete and rapid loss of leaves is however consistent with a lightning strike.



These gaps can also occur in *Bruguiera* stands, seen here in the Merbok mangrove, Malaysia.



These small clusters of dead and completely defoliated *Rhizophora apiculata* trees can often be seen from mangrove streams. These regular round holes are not uncommon and could represent a significant loss in timber production. Over some three decades, we have inspected hundreds of these gaps (many, newly formed) but have never seen any burn or scorch marks. Our clincher which confirms that the gaps are not caused by lightning is finding such a gap under a power-line tower with power lines. The tower and power lines would have acted as a most effective lightning conductor, and we cannot imagine how lightning can create a gap under such conditions.



A *Rhizophora apiculata* gap in the Merbok mangrove, next to a power-line tower with power lines. This photograph looks like being the clincher, confirming that the gaps are not caused by lightning!

The question then is: if it is not lightning, then what?

First, circular holes are often associated with the pattern of fungal growth; so a fungal infestation of the root from a central spot spreading out is a possibility. Except that here, there is no spread, radiating from a central tree. Instead, the cluster of plants appears to lose their leaves together, as seen from the sudden defoliation. We do not know of any studies on fungal infestation of *Rhizophora* roots.

Our first clue for an alternative explanation was when Jean Yong (who had worked with Murphy at the National University of Singapore but now at the Singapore University of Technology and Design) kindly informed us that stem-boring beetles were likely involved and directed us to Murphy (1990). However, Murphy (1990) had only alluded to the twig borer as sometimes attacking *Rhizophora: 'Twig borers are not normally significant on Rhizophora except Avicennia and Sonneratia are heavily attacked by Zeuzera conferta.'* Jean Yong (pers. comm.) has since clarified that their subsequent studies (unpublished) have shown that the infestation is much more significant than Murphy first thought.

A question still remains: borer attacks usually result in damage just to twigs and branches rather than to whole trees. Gill & Tomlinson (1971) have shown through pruning experiments that bud primordia are suppressed so new shoots do not form after heavy pruning: 'on axes more than 1 cm in diameter and more than three years old, suppressed buds are incapable of growth.'

But this still does not answer the question of why whole trees defoliate, losing their leaves all at once. Why are trees of other species adjacent to the gaps not affected?



A gap in Matang where the standing dead trees are those of *Rhizophora apiculata*. Other tree species such as *Sonneratia* and *Avicennia* including *Acrostchum aureum* (the mangrove fern) in the foreground are unaffected.

Our hypothesis is that water in the xylem vessels of the Rhizophoraceae are under very high tension (Ong et al., 1995) so that if enough of these water columns are broken (please see Clough, 2013 for details on xylem vessel embolism and cavitation), water can no longer be delivered to the shoots. Leaves will quickly dry and drop, as observed in these gaps. This may explain the mass defoliation and mortality of trees when these gaps are formed.
Unsustainable and Conversional Use

Although it is possible to manage mangrove forests on a sustainable basis, many mangrove forests are still being destroyed or degraded in the process of timber harvesting (e.g. by the mangrove woodchip industry). The other problem is that the mangrove ecosystem has roles other than just the production of timber, and management schemes should consider these other roles.

The main reasons mangroves are still being destroyed or degraded at the present high rate of about 1% per annum are two-fold: i) the burgeoning population pressures in most of the developing countries where mangroves are located, and ii) the very low value placed on mangrove land (e.g. Ong et al., 2001; Dodd & Ong, 2008).

Not much can be done to save the ecosystem from human population pressures: this is a simple case of exceeding the carrying capacity of a natural resource, resulting in the destruction of the ecosystem. The root cause of this problem is the inability to regulate the growth of human populations in developing countries.

Mangroves are exploited for their timber, which is used mainly as fuel wood (directly as firewood or converted to charcoal), as poles (mainly for pilings), and as mangrove woodchips (for the production of rayon). It has been clearly demonstrated that mangroves can be sustainably managed for the production of timber but the mangrove woodchip industry has a very poor record when it comes to sustainable management. The other problem is that mangrove timber appears to be undervalued. The woodchip market is essentially a monopoly and the price of charcoal (traditionally used as fuel) is based on historical factors.

Apart from the low values of actual products, other values (e.g. contribution to coastal fisheries and biodiversity) have not been considered when mangrove ecosystems are destroyed or degraded in the process of timber extraction. This basic problem is one of the failures of our economic system to account for non-market values. Yet, mangroves account for only a couple of percent of the earth's land area, which makes them very valuable simply because of their scarcity.

Mangroves have been traditionally considered waste land, better to be reclaimed and converted to other uses. This view has been demonstrated to be mistaken but the low value persists. For instance, although most mangrove lands are susceptible to acid sulphate conditions and are thus not very suitable for conversion to aquaculture ponds, they are still being put to this use, mainly because of the low cost of acquiring mangrove land compared to land in surrounding areas.

The problem is not one of just being able to put values to different components of the system; it is basically an economic, not an accounting problem. This calls for a major paradigm shift.



Much of the world's tropical mangroves have been extensively converted to shrimp culture ponds in the past three or four decades including the Merbok mangrove in Malaysia (top). Conversion of mangroves to shrimp aquaculture and rice cultivation (bottom left), and for residential development (bottom right).



These shrimp ponds, constructed within a protective coastal fringe of mangroves (top), have been eroded away though natural geomorphological processes (foreground). This is on the low-energy coast bordering the Straits of Malacca. It is much wiser and more efficient not to allow development in a buffer strip at least some tens of metres from the highest tide mark. Such old bye-laws exist but are seldom enforced. Landward encroachment of oil palm plantations into the mangroves, Malaysia (bottom).

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