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Gaps in mangrove science

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Abstract As tidal forest found on tropical and subtropical coastlines, mangroves have long attracted scientists, yet gaps in our knowledge remain. Perhaps reflecting the many and variable ways in which ecological conditions exist and factors may interact in the intertidal environment, uncertainties and debate are evident at mangrove conferences. Even core issues, such as salinity tolerance, and what constitutes a ‘true’ mangrove, endure. This paper seeks to review the gaps in mangrove science and do so in a way that may stimulate further research. Aspects of mangrove flora such as ‘true’ vs. ‘associate’ mangrove and the species concept open the discussion. Some very basic biological processes, such as age and wood, phenology and root system vs. shoot system biomass allocation, follow. These lay the foundations for a survey of ecological processes and challenges including salinity tolerance, soil redox conditions, temperature limitations, propagule dispersal, mineral cycling, carbon sequestration and land building. The older topic of mangrove succession and the very neglected question of pathogenic *Phytophthora* in mangroves are also examined. Collectively, the above biological and ecological gaps in our knowledge provide a platform on which mangrove goods and services and applied sciences can be evaluated. Into these topic areas come the urgently needed economic valuations of mangrove resources in fisheries and coastal protection, together with their largely unheralded potential as a bank of biomedical and bioactive compounds. Finally, contentious issues such as using (or mis-using) mangroves as sinks for industrial waste and how much biodiversity is needed to maintain functionality in mangrove eco-restoration are examined. Some apparently small but nevertheless attractive topics like tiger and dolphin conservation and mangroves as food also appear and serve to illustrate the sometimes subtle interconnections within mangrove ecosystem science.

Keywords: Mangrove science, gaps, above ground versus ground biomass, salinity tolerance, land building, valuations, bioactive extracts, eco-restoration.

1. Introduction

Despite a long interest in mangrove science by biologists and foresters that spans a 100 years or more, many gaps in our knowledge remain. Some of the uncertainties about core issues such as salinity tolerance and what constitutes a ‘true’ mangrove still endure. Notions of these core aspects can be found in Watson (1928), Macnae (1968), Chapman (1976), Tomlinson (1986), Hutchings & Saenger (1987) and Aksornkoae *et al.* (1992). Even in recent impressively comprehensive books such as Saenger’s (2002) *Mangrove Ecology, Silviculture and Conservation*, and Alongi’s (2009) *Energetics of Mangrove Forests*, the data on just how salt tolerant a given mangrove species is, remains variable and inconsistent. Such inconsistency and variability in the range of salinity tolerance observed demonstrates that the interaction of a host of environmental factors occurs and that much more remains to be done on the finer points of mangrove eco-physiology. The question of what exactly is a ‘true’ mangrove vs. a so-called ‘associate’ mangrove is very much alive and, once again, attracted discussion and debate at the recent international series of workshops on a Trans-boundary Diagnostic Analysis of Indochina Mangrove Ecosystems (TBDA) held at the Sirindhorn International Environmental Park (Macintosh *et al.*, 2013). The topic of ‘true’ or ‘exclusive’ vs. ‘associate’ or ‘non-exclusive’ mangrove is far more than academic. In today’s world of storm or tsunami damage and human destruction (sometimes hidden under the words ‘reclamation’ and ‘conversion’) of mangrove ecosystems, the need to know which mangrove species is best for an eco-repair and restoration project is of paramount importance. This importance must be measured in both ecological and economic terms.

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At the heart of this review lies the aim to identify some of the important gaps that still exist in our science of mangroves and do so in a way that may be helpful in the stimulation of further research endeavour. It is thought that the following sequence of topics may provide a useful logic. Aspects of mangrove flora covering the species concept and the on-going debate related to 'true' versus (vs.) 'associate' mangroves will be addressed first. This will set the scene for a look at some biological processes like phenology, wood and mangrove age; ecological processes involving challenges such as salinity vs. redox, chill tolerance, mineral cycling and fungal pathogens. Within this process section, older ecological concepts – which are still alive in mangrove science – like succession and the importance of buoyant propagules will also be visited. Against this background of gaps in mangrove science, the last two sections will cover aspects of applied science like eco-restoration and the neglected yet stimulating areas of mangrove linguistics and the sociology of science as it exists in the context of mangrove studies. Thus, it is hoped that a review of this nature will appeal to the diverse array of mangrove disciplines such as biological sciences, chemistry, ecology, economics, forestry, geology and geography, physics, sociology and zoology. To facilitate this broad potential appeal, the writing style used will be more like that of a general textbook rather than that of a technical paper aimed at a limited peer group readership. In addition, since many topic areas are interconnected there will be some overlap as the discussion unfolds.

2. Mangrove flora: Definitions, categories and the species concept

2.1 Mangrove defined

Even in the most recent of publications, one can still find definitions of what a mangrove is, that must attract critical comment, e.g. Naskar & Palit (2015) in their review of the 'anatomical and physiological adaptations of mangroves', who stated that mangrove refers to woody plants of intertidal forest communities. More acceptable and inclusive definitions follow those of field based ecologists such as Primavera *et al.* (2004) who, correctly in my assessment, define mangroves as higher plants – trees, shrubs, palms, herbs or ferns – that predominantly grow in the intertidal areas of tropical and subtropical shorelines. As we shall see later, the mangrove fern, *Acrostichum* spp., is very much a mangrove, I am surprised that it was not included in the above-mentioned review. This interesting and inviting case of the mangrove fern receives a more complete treatment in section 3, where I consider ecological processes and challenges facing life in the intertidal environment.

2.2 Categories: 'True' vs. 'associate' mangroves

Despite the fact that up to 84 species of plants have been recognized as mangroves (Saenger, 2002), an inspection of the literature will reveal that debate and disagreement still occurs when mangrove scientists attempt to assign 'true' vs. 'associate' status to many mangroves. Some follow Tomlinson (1986) and appear comfortable with a two-way categorization of mangroves as either 'true' or 'associate' (e.g. Primavera *et al.*, 2004; Kitamura *et al.*, 1997; Hong & San, 1993). Others, in contrast, prefer to talk of 'exclusive' vs. 'non-exclusive' mangroves. This latter group have also been termed 'back' mangroves – a reference to their typical occurrence towards the landward end of an intertidal mangrove forest. Here, the term ecotone species would be more appropriate and has been used at various Ecotone Conferences (e.g. Maxwell, 1995).

Discussions and debate relating to ideal mangrove species as candidates for eco-restoration projects, which occurred during the major Trans-boundary Diagnostic Analysis (TBDA) of the present condition and need for eco-rehabilitation of Indochina Mangrove Ecosystems (Macintosh *et al.*, 2013), underscored the need to do much more research on mangrove eco-physiology. With more knowledge of individual species tolerance of major environmental factors as salinity, soil redox conditions (anoxia), sedimentation rates and temperature, these on-going debates about so-called 'true' vs. 'associate' mangroves should fade. One of many positive outcomes from enhanced knowledge in this topic would be a move to encourage better biodiversity in mangrove eco-restoration schemes.

2.3 Species concept

In mangrove science, the species concept appears to be used correctly in some important writings, e.g. Saenger (2002), where genetic isolation is employed as the core component of the concept. In an analysis of hybridizations within the mangrove flora, Saenger (2002) pointed out that uncertainties remain concerning the few cases of hybridization that have been reported. Perhaps the best known case of these uncertainties is that of *Rhizophora annamalayana*, a 'new species' of mangrove from southern India, described by Kathiresan (1995), which was later, on the basis of mitochondrial DNA studies, thought to be a sterile F₁ hybrid between *Rhizophora mucronata* and

Rhizophora apiculata (Parani *et al.*, 1997). It is tempting and perhaps wise to follow the suggestions of Ballment *et al.* (1988), Parani *et al.* (1998) and Abeyasinghe *et al.* (1999), and conclude that genetic isolation between most mangrove species is complete. Discussing the questionable status of a 'new' *Kandelia* species, *Kandelia obovata*, Maxwell (2007) pointed out that while variation existed within geographically isolated populations of *Kandelia candel*, these were best described as ecotypes rather than 'new' species (Figure 1). Recent observation with long-term transplants of *K. candel* ecotypes from Brunei and Thailand to Hong Kong have shown all of these ecotypes to be inter-fertile, thus confirming their one species status. In short, the designation of *K. obovata* is premature and invalid.

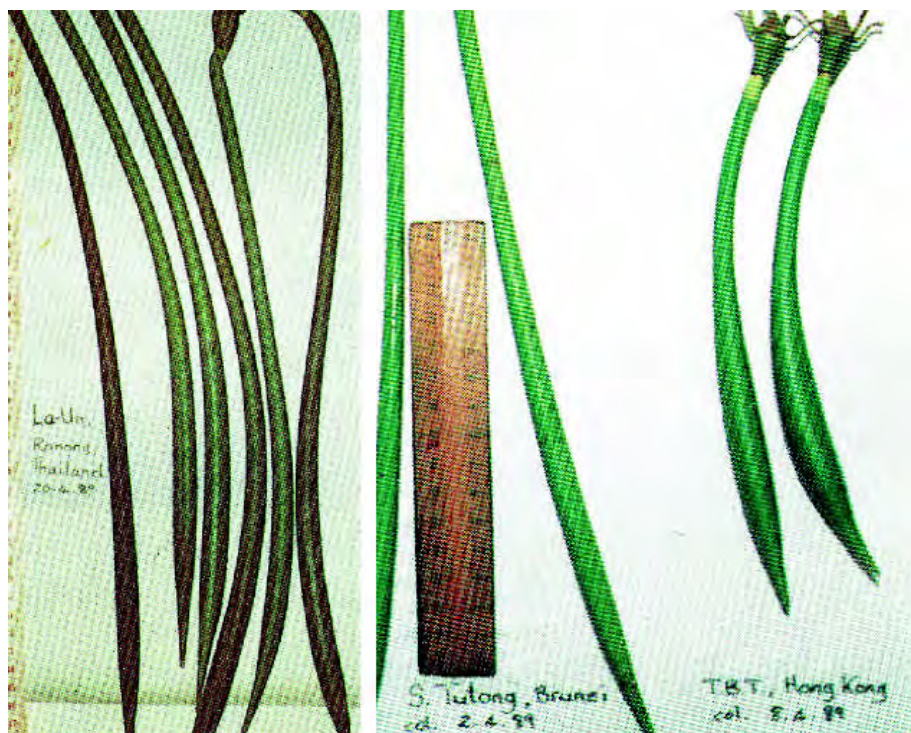


Figure 1 *Kandelia candel* ecotypicity expressed in the morphology of propagules: same species but different expression of biological potential (La-Un, Ranong Thailand; Sungai Tutong, Brunei; and Tsim Bei Tsui, Hong Kong)

Sadly, we are inclined to contrast the way the species concept is sometimes inconsistently applied in mangrove biology with what are normally considered reliable and well-accepted definitions of a biological species in the more general literature. Clugston (2009) defined species as a population of individuals that share a high degree of common characters and interbreed to form fertile offspring. Likewise, Dobson (1998), Bush (2003), and Smith & Smith (2009) defined species and speciation in terms of reproductive isolation.

As will be argued when ecological challenges are reviewed, mangrove plants do face, on a daily basis, a rather unstable environment. This is especially the case in terms of salinity, substratum and sunlight. Not surprisingly perhaps, one finds ecotypes (Maxwell, 1995, 2007), ecological varieties (Kathiresan, 2010) and geoforms (López-Portillo & Ezcurra, 1989). In the absence of careful inter-fertility studies, it can be tempting to see such ecotypes and geoforms as 'new' species, when, in fact, they may be nothing more than the expression of phenotypic plasticity inherent within a specific genome.

3. Biological processes

Some basic gaps remain in our knowledge of biological processes in mangroves. They include:

3.1 Age and wood

There is a serious shortage of data on how to age a mangrove tree or shrub from seasonal wood rings ('annual rings') patterns in the xylem. This was noted as an area inviting attention by Chapman (1976), and unpublished data from New Zealand populations of *Avicennia marina* had ~2.1 wood rings, indicating growth periods occurred annually.

Thus, single, individual ‘annual rings’ were absent (Maxwell, unpub. data, 2008). This observation is worth further study as the data on what both Chapman (1976) and Saenger (2002) described as the anomalous wood structure of *Avicennia* is rather old and limited (Gill, 1971). Nevertheless, this topic is far more than a source of fascination for a few keen students of plant anatomy. Wisely, Saenger (2002) pointed out that because of *Avicennia*’s anomalous distribution of xylem and phloem tissue (non-annual growth rings of alternating bands of xylem and phloem), *Avicennia* cannot be killed by ring barking, which may be in terms of life in the intertidal zone, a useful adaptation to cope with damage from waterborne objects. The long-term, painstaking, often invasive and sometimes destructive nature of wood age work may be a disincentive to research effort in this interesting topic.

3.2 Phenology of mangroves

The recent paper by Kamaruzzaman *et al.* (2013) indicated that mangrove phenology, especially reproductive phenology, remains an area where more investigation is required. One key observation that provokes speculation and invites research is the extremely low conversion rate of flowers to mature propagules (Table 1). Factors responsible for this low conversion are unknown. Hypotheses to help ‘explain’ the situation include nutritional shortcomings, poor flow adaptations to wind or animal pollination and the lack of suitable pollinators in the mangrove area under study. Wee *et al.* (2014) working with Singaporean mangroves in what they called small urban stands of mangrove suggested that *Bruguiera gymnorrhiza*’s low fruit yield may be due to reduced pollination visitation by nectar-seeking birds – a problem linked to the small (~ 5 ha) size of the mangrove stands.

Table 1 Conversion rates (%) of flowers to mature propagules of mangrove species in selected areas

Species	Location	Conversion (%)	Reference
<i>Avicennia marina</i>	Brunei	1.5	Maxwell (1993)
<i>Kandelia candel</i>	Brunei	2.3	Maxwell (1993)
<i>Rhizophora stylosa</i>	Okinawa, Japan	2.5	Kamruzzaman <i>et al.</i> (2013)
	Darwin, Australia	0.5	Coupland <i>et al.</i> (2006)
	Viti Levu, Fiji	0.8–2.1	Tyagi (2003)
	Hinchinbrook Island, Australia	1.5	Duke <i>et al.</i> (1984)

Clearly, mangrove phenology displays vacancies for research input. The information gained would be welcomed by those involved in mangrove restoration and silviculture as supplies of propagules become limiting factors in their work. A research focus that included more of the less abundant and less popular mangroves would be most helpful due to the need to restore degraded mangroves with adequate biodiversity. Climate change challenges also mean that to rely on a narrow species pool of mangrove would be unwise.

3.3 Root system and shoot system biomass allocation

Mangrove scientists have asked the question, do mangroves allocate more biomass below ground than above ground? It has been thought that they do. But this, too, has been questioned and some have speculated that mangroves are not much different from terrestrial trees and shrubs in how they allocate root vs. shoot biomass (Alongi, 2009). However, this may be the wrong question, as in a typical mangrove environment, the soft unstable substratum is such that a lot of root biomass is, in fact, above ground. Therefore, a more apt question is that of above ground biomass vs. below ground biomass. Alternatively, an effort should be made to clearly define what root biomass is. This may include an above ground and a below ground component. It appears that published data on above ground biomass (AGB) vs. below ground biomass (BGB) are few (Alongi, 2009). One of the reasons for this is practicality: obtaining BGB data from a mangrove habit is very difficult practically. Few studies of actual root biomass have been made as they are labour intensive, destructive and time-consuming. One compromise method that gave the sampled mangrove trees a good chance of post-sampling recovery was the trench method (Komiyama *et al.*, 1987). Sampling whole plants of *A. marina* in Hong Kong, Maxwell (1993) found the combined above ground root biomass (AGRB) and below ground root biomass (BGRB) to be 51.64% while the stem (including leaves and twigs) above ground biomass accounted for 47.15% of the total shrub biomass. Similar values were obtained for *K. candel* in

the same study. Clearly, there were important differences between root (AGRB + BGRB) and stem ratios. These Hong Kong mangroves were small shrubs (0.3–0.4 m tall) that reflect the climatic limitations (cool, relatively dry winters) of south China (Hodgkiss, 1986, 1997). Old (>20 year), squat, compact shrubs can be just 0.3–0.45 m tall and few reach around 3 m in height (Maxwell, 1993). The same species are taller with more biomass in Thailand (3–6 m in height for *A. marina* and 4 m for *K. candel* as is the case for many truly tropical mangroves (Aksornkoae *et al.*, 1992). Size would be expected to influence root vs. shoot allocations, but the matter is far more complex than pure tree size. The degree of substratum anoxia may have an important influence on root system vs. shoot system biomass allocation. Curran *et al.* (1986) showed that under lab conditions, root system vs: shoot system ratios in *A. marina* varied from 0.5–1.1 depending on the degree of anoxia during growth.

Clearly, more investigation – in both the lab and field – would help to resolve the question of biomass allocation in the above and below ground parts of mangrove trees and shrubs. Those mangroves that tend to make more above ground root material as prop and buttress root supports may be more useful as candidate species in coastal protection and at locations where sea level rise is expected.

4. Ecological processes and challenges

As mentioned in section 1.1, the mangrove fern *Acrostichum* has been overlooked in a recent review of mangrove adaptations and was considered a ‘mangrove associate’ by Tam & Wong (2000) but a ‘true mangrove’ by Kitamura *et al.* (1987) and Maxwell (2002a). In section 4.3, this fern again attracts discussion in the context of under-storey species as part of mangrove forest structure. Saenger (2002) noted *Acrostichum* presence as an under-storey mangrove suggesting that it may compete at sites where reduced salinities exist. Wisely, Saenger (2002) was somewhat tentative in designating *Acrostichum* into any particular ecological category as in terms of photosynthesis efficiency in the field, *Acrostichum speciosum* is similar to other mangroves, including what some workers continue to describe as ‘true’ mangroves. As hinted earlier, this remarkable fern with a gametophyte that copes with salinity (Nakamura, pers. comm.), introduces us to the long-standing and yet still only partly understood issue of salinity tolerance as a major ecological challenge facing mangroves.

4.1 Salinity tolerance: Still only partly understood

Mangroves with good salinity tolerance are those that can to some extent control salt intake and maintain a water balance that is physiologically acceptable (Saenger, 2002). However, although a general understanding of how salinity tolerance is achieved is known, many details remain incomplete and the findings can be variable and inconsistent. Gray *et al.* (2010) expressed this situation in stronger terms by contending that many myths still remain concerning the halophytic nature of mangrove physiology. These workers cite the sacrificial leaf hypothesis (excess salt is deposited in old leaves that are later shed) as a good example of such a ‘myth’. To support their rejection of the sacrificial leaf hypothesis, they reported that both red (*Rhizophora mangle*) and black mangroves (*Avicennia germinans*) do not especially deposit salt in senescent leaves. They found no differences between salt levels in young vs. old leaves.

As indicated earlier, the mangrove fern *Acrostichum* provides an excellent example of this situation as the limited literature on this fern is peppered with different and contradictory findings on its salinity tolerance together with its adaptations in terms of ecological anatomy and physiology. The fern has been variously described as an under-storey plant in mangroves where the salinity is reduced (Saenger, 2002), a hardy fern, an opportunistic disperser able to colonize canopy gaps in a typical tropical mangrove forest, a biotic factor influencing mangrove succession (Havanond, 2002) or a ‘mangrove associate’ (e.g. Tam & Wong, 2000) and therefore somehow not really a mangrove at all and a mangrove weed or ‘vegetable pest’ (Watson, 1928).

Yet despite these variable viewpoints, some research shows that *Acrostichum aureum* (one of the two mangrove ferns) has, in fact, a wide tolerance range in terms of light and soil salinity (Medina *et al.*, 1990). Working with the Hong Kong mangroves, Hon (2005) found that this species could tolerate full sunlight and high salinity (~32 ppt), and had a well-developed aerenchyma in its root tissue – another clear indicator of mangrove adaptation. Balasubramanian *et al.* (1992) linked *Acrostichum*'s frond content of cyclitol (low molecular weight carbohydrate) to its osmo-compensation ability. Thus, it appears that the mangrove fern may have, like *K. candel* (aka *K. obovata*) (Maxwell, 2007), interesting ecotypic plasticity.

4.2 Salinity tolerance: More field and lab data are needed

Alongi (2009) usefully generalized that growth responses to salinity vary greatly, reflecting a wide range of tolerance among species. This may, simply, reflect in-built tolerance mechanisms but it may also indicate that we cannot be totally confident with our general understanding mentioned earlier (section 4.1). It remains unclear if any mangrove is an obligate halophyte (Alongi, 2009). Indeed, when one reads statements such as, 'some species such as *A. marina* do not grow in fresh water and *may* (italics are mine) be obligate halophytes' (Alongi, 2009), one could be justified in concluding that we simply do not know if any mangrove ('true' or otherwise) has an obligate requirement for salt in order to survive and reproduce. The same author quotes Clough (1992) as suggesting that others (we should ask, 'which others'?) survive well in fresh water and *may* (italic is mine) not have an obligatory requirement for salt beyond a trace amount! What exactly are trace amounts? Some impressive data have appeared in book-sized reviews of mangroves and maximum salinity tolerances, but what a designation like 'relative salinity tolerance' means in relation to this data is unclear (Table 2).

Table 2 Sample of salinity tolerance data

Species	Maximum soil salinity (ppt)	Reference	Relative salinity tolerance	Reference
<i>Acanthus ilicifolius</i>	65	Saenger (2002)	++	Alongi (2009)
<i>Aegiceras corniculatum</i>	148	Saenger (2002)	+++	Alongi (2009)
<i>Avicennia marina</i>	300	Saenger (2002)	+++++	Alongi (2009)
<i>Bruguiera gymnorrhiza</i>	85	Saenger (2002)	+++	Alongi (2009)
<i>Lumnitzera racemosa</i>	110	Saenger (2002)	++++	Alongi (2009)
<i>Kandelia candel</i>	44	Maxwell (1993)	+++	Alongi (2009)
<i>Bruguiera sexangula</i>	31	Aksornkoae <i>et al.</i> (1992)	+	Alongi (2009)
<i>Sonneratia caseolaris</i>	31	Aksornkoae <i>et al.</i> (1992)	+	Alongi (2009)
<i>Nypa fruticans</i>	31	Aksornkoae <i>et al.</i> (1992)	+	Alongi (2009)

Salinity tolerance ranges from +++++ (very tolerant) to + (not tolerant)

From the relative tolerance table given by Alongi (2009) where the mangroves *Bruguiera sexangula*, *Sonneratia caseolaris* and *Nypa fruticans* were described, it is unclear what 'not tolerant' means. In fact, all of these three mangroves can tolerate salinity of around 20 ppt (Maxwell, 1993). Clearly, the data given by Saenger (2002) ([S] in Table 2) shows that some mangroves have the ability to grow and survive at salinities sometimes above that of oceanic seawater (35 ppt or 3.5% salt), and in some cases over eight times that of oceanic seawater (30% salt) as in the case of *A. marina*. Table 2 indicates that this old salinity tolerance issue is far from closed.

What would be of most interest to further research are the consequences of surviving in hypersaline soils. As Saenger (2002) pointed out there is a cost to pay by the mangrove when surviving in hypersaline soil and typically this cost comes as inhibited growth. Extending this idea, Saenger (2002) suggested that a species may opt for salt tolerance and thus extend its habitat range along saline soil gradients or opt for more rapid growth and therefore competitive ability under lower salt conditions. To opt for both 'strategies' would be impossible. Interpretations of the variable and at times seemingly contradictory data on mangroves and salinity like those attempted by Saenger (2002) and briefly hinted by Alongi (2009) are strong invitations to do much more work on the eco-physiology of mangroves. Not surprisingly, the recent review by Naskar & Palit (2015) commented that the question of how mangroves organized themselves to maximize carbon gain and minimize water loss, needs more critical study. The environmental challenge of salinity is a key factor in water availability for photosynthesis.

Surprisingly for those who are in forestry and plant eco-physiology, above ground roots also can make important contributions to total plant photosynthesis. Moreover, the ability of these above ground photosynthesizing roots to add oxygen directly into below ground roots enables mangroves to cope with at least some daily water-logging (Dromgoole, 1988). Here, again, is an interesting physiological adaptation worthy of more research.

4.3 Salinity and redox conditions

Rates of water uptake tend to be lower in waterlogged mangroves than in those grown in aerobic conditions (Youssef & Saenger, 1998), and salinity tolerance is reduced under anaerobic conditions caused by water-logging (Saenger, 2002). Redox values in anoxic soils can be low (e.g. <400 mV) and inhibit mangrove sapling growth, especially when salinities in subsurface soft sediments are around 36 ppt (Havanond *et al.*, 1997).

From the still limited work done on the relative importance of salinity vs. redox conditions, more study of the impact that high salinity (>35 ppt) but low (0–100 mV) redox values in mangrove mud compared to low salinity (1–15 ppt) but high redox values (>400 mV) would be of value and may help increase success rates in mangrove rehabilitation schemes. Some of these have been expensive failures due to planting mangrove seedlings or propagules in inappropriate sites (Macintosh *et al.*, 2013).

4.4 Mangroves and temperature

In a comprehensive survey of this topic, Saenger (2002) made an interesting observation that the ecological response of mangroves to high air or water temperatures (i.e. around 35°C) is not well known. Mortality for *Rhizophora stylosa* occurs when substratum or water temperatures reach ~40°C (Baba, 2011). With low temperatures, the limited results are rather incomplete: Chapman & Ronaldson (1958) considered that the world's southernmost mangrove, *A. marina*, was limited in its biogeographic range by the number of killing frosts, i.e. around -3°C. Maxwell (1971, 1986, 2002) gained experimental evidence in the field that supported Chapman & Ronaldson's viewpoint. Interestingly, Maxwell's (2002b) field investigations were with Hong Kong and Thai ecotypes of *A. marina* and only the Hong Kong ecotypes could withstand an overnight chill shock of 3.8°C. The Thai *A. marina* seedlings displayed blackened foliage within a few days after the cold snap and were completely defoliated within two months after the twin cold overnight episodes. *K. candel* is known to be the only other mangrove species to be classified as cool-temperate and this species marks the northern biogeographic distribution of mangroves (Maxwell, 1995).

4.5 Mangrove dispersal: Propagule buoyancy

As with many topics in mangrove science, this seemingly straightforward topic has generated debate and alternative viewpoints for decades (e.g. Guppy, 1906; Muir, 1937; MacNae, 1968; Chapman, 1976; Maxwell, 1993; Saenger, 2002). Nevertheless, there seems to be an enduring opinion that continues to support the idea that key mangrove species disperse using buoyant propagules and can do so over considerable distances.

Not surprisingly perhaps, there is very limited experimental data to enable us to decide whether mangrove propagules could be a key biogeographically important adaptation for species dispersal. What little exists gives an inconsistent picture. For example, Ball & Pidsley (1998) reported that propagules of *A. marina* could float for at least six weeks while Clark & Myerscough (1991) had evidence that propagules of this species could float for just 24 hours. This latter finding seems to have encouraged Duke (1995) to argue that such propagules would be unable to cross sea distances of more than 200 km. Surprisingly and in contrast to the claim by Clark & Myerscough (1991), Rabinowiz (1978) reported that the related *A. germinans*, can float for up to 82 days. Using *A. marina* again, Maxwell (1993) showed that propagules could retain buoyancy for 80 days in lab seawater with 66% viability. Propagules of *K. candel* could float for 258 days in seawater.

From these experimental results, it seems that while contradictory findings do exist in the literature, the potential for oceanic dispersal of mangroves is very real and an area awaiting more investigation especially with mangroves that produce viviparous seedlings sometimes having fleshy cotyledons like *Avicennia* or prominent radicles like *Rhizophora* and *Kandelia*.

4.6 Mineral cycling

Alongi (2009) made an impressive attempt to draw generalizations from the very limited information available on cycling of essential elements such as iron, potassium, sodium, magnesium, calcium, zinc, copper, manganese and vanadium in mangrove systems. On close examination of the data presented for leaf litterfall from three Chinese mangroves (*K. candel*, *B. sexangula* and *R. stylosa*) by Li (1997) and Lin (1999) appears surprising, e.g. in *R. stylosa* the turnover time of calcium was cited as taking ~42 years, while that of magnesium only ~15 years. Those of *Kandelia* were four times shorter with a turnover time for calcium of only ~7 years (in huge contrast to that of *R. stylosa*) and magnesium being shorter than *R. stylosa* at ~12 years. Such data seem surprising since both calcium and magnesium feature in leaf cell structure as key elements in cell walls and chlorophyll pigments. So why would the calcium turnover time be almost three times as long as that of magnesium in *R. stylosa* leaves and so fast in *K. candel* leaves? Furthermore, the turnover rates reported here are hard to reconcile with the phenology of leaves in these or similar species (Leung, 1986 in Hong Kong, Boonruang, 1978 in Thailand, and Kamaruzzaman *et al.*, 2013 in Okinawa) where one-year cycles were observed. Wisely, Alongi (2009) further cautioned that there remains an urgent need for complete ecosystem-level budgets of essential elements in mangrove systems. When one looks at network models of mangrove ecosystems one can find some attractive attempts to link litterfall dynamics to energy flux budgets, but assumptions of linear relationships and steady-state conditions exist (Alongi, 2009). In my view, it is most important to make such assumptions and their limitations clear. It would be ideal if more fieldwork was conducted to add stronger injections of reality to the challenging areas of mineral cycling and energy flow.

4.7 Mangroves as carbon sinks

The importance of mangrove forests as valuable carbon sinks is still to be more fully assessed, but it is given as a highly desirable ecological function along with other eco-economically important roles such as flood control, storm protection, water quality maintenance, fishery support and ecotourism (Macintosh *et al.*, 2013). One of the abiding problems with this positive role of mangroves as carbon sinks is the need for more hard-won convincing data. The requirement for more complete studies was demonstrated recently by Rodrigues *et al.*, (2014) who clearly showed that carbon content not only varied by mangrove species but also according to plant parts. In their analysis of three Brazilian mangroves (*Avicennia schaueriana*, *Laguncularia racemosa* and *R. mangle*), they showed generic whole plant estimates of carbon stock (sequestration) may be incorrect by ~13.6% for above ground biomass and by ~25% for root biomass. These differences were attributed to the allocation of different amounts of carbon into woody stems, leaves and root biomass. Carbon sequestration varies by species and by plant parts. Of much interest was the finding that woody parts (trunk, branches and prop roots) and roots accounted for between 84% and 86% of these trees. These are the longer-lasting components, and if such woody material and the roots were used in non-destructive ways (e.g. as construction material) and therefore not returned to the atmosphere via combustion, the carbon capture values of these mangroves would be considerable. Perhaps one of the best approaches to the carbon sink role would be to align this with as many other positive eco-economic roles of mangrove ecosystems as possible. Such mangrove valuations would clearly illustrate the \$ value of mangrove services.

4.8 Mangroves as land builders

The role of mangroves in sediment regulation has been recognized for some time (Saenger, 2002), and a small bank of data from various locations around the world on mangrove sediment accretion rates is available (Table 3). As can be seen from an inspection of the data in Table 3, mangrove ecosystems can play a role in land building. In short, they can enhance sedimentation. In the face of what organizations such as the IPCC (Intergovernmental Panel on Climate Change) predicted that global sea levels are on the increase and are expected to rise from 0.15 m in 2000 to 1.0 m by 2100. Even if these estimates were shown to be too generous, the potential for mangroves to assist in shoreline stabilization, sedimentation and land building is real. Such a scenario is of particular relevance to the populated coastlines of tropical and sub-tropical Asia. For many in these regions, sedimentation may have some advantages and perhaps the advantages of coastal protection, sedimentation and land building together with other values of mangrove assets (e.g. fisheries) outweigh any disadvantages.

Table 3 Mangroves and sedimentation

Location & coastal environment	Increase in sediment depth (cm/yr)	Accretion	Reference
Cairns coast, Queensland, Australia Depositional deltaic plain at Barron River with extensive mangroves of <i>Avicennia marina</i>	0.80	Episodic, ~60 m in 30 years	Bird (1992)
Kosrae Island, Micronesia Mangroves formed along coral reef coast	0.10–0.20	Steady rate over the past 2000 years	Fujimoto et al. (1996)
West coast, Peninsular Malaysia Mangrove forests occur at Pulau Langkawi, Sungai Merbok, Matang and Sungai Pulai	No specific information	Cyclic, accretion at >15 cm/yr coupled with erosion at ~8 m/yr	Teh & Lim (1993)
Piako River, Hauraki Plains, New Zealand Estuarine mangroves of <i>Avicennia marina</i>	0.64	Accretion of ~200 m in the last 50 years	Young & Harvey (1996)
Waiheke Island, Auckland, New Zealand Mangroves of <i>Avicennia marina</i> along tidal creeks	0.31	No specific information	Maxwell (1984)
Deep Bay, Hong Kong Mudflats and mangroves of <i>Avicennia</i> and <i>Kandelia</i>	1.10	Accretion of 7.6 cm/yr	Duke & Khan (1999)
Sai Wan, Sai Kung East, Hong Kong Mangroves of <i>Aegiceras</i> and <i>Kandelia</i> in estuaries and lagoons	0.23	Episodic with gains and losses	Maxwell (2000)
Southeast coast, Thailand Accreting mangrove shores of <i>Avicennia</i> , <i>Sonneratia</i> and <i>Rhizophora</i>	No specific information	Accretion of ~40 m/yr from 1966–1994	Pananitukkul et al. (1998)

Interestingly, in some developed countries, such as New Zealand, the contributions that mangroves make to sedimentation are viewed with displeasure. Indeed, some groups have come to look upon mangroves as ‘pests’, ‘weeds’ or unwanted coastal shrubs trees that cause siltation within marinas, thus hindering water sports (Maxwell, 2006). The root cause of mangrove expansion in northern New Zealand where one species of cold-tolerant mangrove *A. marina* can survive, is not the mangrove themselves but the availability of sediment. Most of the sediment comes from human activity on land of which deforestation and inadequate soil management are prime causal factors. The mangroves are opportunistic land builders or sedimentation agents, not the cause of sedimentation. They may enhance this geomorphological process, but they do not cause it. The negative attitude exhibited by some limited-interest pressure groups in New Zealand contrasts with the strongly pro-mangrove outlook of Japan, such as those in the Okinawa archipelago (Maxwell, 2006).

The data shown in Table 3 show that mangroves do not and cannot operate uniformly in a land building role. A host of geomorphological factors come into play (e.g. Wolanski *et al.*, 1992). Nevertheless, there is room for more research on mangroves’ contribution to sedimentation, to sediment capture and to land building in the face of sea-level increases. Such research presents excellent scope for inter-disciplinary co-operation between the physical sciences (e.g. physics) and biology, and between faculties as may happen when engineers and ecologists focus on complex problems like rehabilitation of degraded shrimp farms: a perfect and much needed focus for eco-engineering.

4.9 Pathogenic *Phytophthora* in mangroves

There is a school of thought that claims that all *Halophytophthora* spp., into which the marine *Phytophthora* spp. have been placed, are non-pathogenic to living leaves and are rather saprobic on submerged fallen leaves (Hyde, 2002). Nakagiri (2002) stated that *Halophytophthora* consists of 14 species of pythiaceous oomycetes that inhabit brackish water in subtropical and tropical mangroves and mainly use submerged leaves as substrate. The same worker also reported that the first *Halophytophthora* was described by Anastasiou & Churchland (1969) as *Phytophthora vesicula* from leaves submerged experimentally in the sea near Vancouver. Later, other species were found e.g. *Phytophthora avicenniae* from Australia. Currently, all these marine *Phytophthora* spp. were put into the genus *Halophytophthora* (Nakagiri, 2002). While there is no need to contend that the newer genus of *Halophytoph-*

thora is questionable, there is a need to question the notion that this genus does not contain a pathogenic member. Maxwell (1968, 1971) demonstrated that at least one strain of *Phytophthora* isolated from *A. marina* roots was pathogenic. Pegg (1980) obtained similar results and concluded that a *Phytophthora* sp. was associated with mangrove mortality in central coastal Queensland. Amazingly, *Phytophthora* spp. were described as being associated with the New Zealand mangrove acting as a host for this pathogen (Chapman, 1975), yet these observations from New Zealand and Queensland were not mentioned in Hyde (2002). It appears that they may have been missed. Thus, more work on *Phytophthora* or *Halophytophthora* as mangrove pathogens would be a fruitful line of investigation, and may even determine that this infamous plant destroyer could play a role in mangrove population dynamics.

4.10 Mangrove succession

The status of mangrove succession seems to hold a relatively low position in mangrove ecology these days. The concept is largely sidelined and replaced in importance by zonation in Saenger's (2002) exhaustive synthesis of mangrove ecology. This point has been made much earlier in accounts of pattern and process within mangrove ecosystems, e.g. by Hodgkiss (1986). In a similar comprehensive review of mangrove forest energetics by Alongi (2009), which complemented that of Saenger (2002), succession is not given thematic treatment as a topic in mangrove ecosystem dynamics but wisely mangrove forests are described as mosaics of interrupted or arrested successional stages. The concept is alive and well-documented in general texts of ecology and continues to be seen as a component of ecological pattern and process (e.g. Smith & Smith, 2009) in long-term studies of ecosystem dynamics. However, the treatment of succession in such general texts does not usually reach mangrove forest ecosystems. To fully describe and explain this apparent neglect of succession in mangroves is well beyond the parameters of this review. What the situation does indicate, however, is that gaps in our knowledge of the place, status and certainly of successional change do exist in mangrove science.

Mangrove ecosystems are often unstable and tend to accelerate sedimentation or land building (section 4.8) and can be the cause of their own demise, once the sediment level reaches a stage where regular tidal inundations are impossible, then mangrove vegetation can give way to ecotonal semi-terrestrial habitats (Zhang *et al.*, 2009). If this land aggradation process is sustained, then succession to coastal terrestrial vegetation will ensue (Chapman, 1976). To some important extent, mangrove succession is dependent on sedimentation and accretion that curtails tidal inundation and moves a given mangrove habitat away from the tidal zone. As shown in Table 3, while sediment build up is often a feature of mangrove-dominated intertidal zones, this is not uniform. The pattern is typically episodic. Alongi (2009) expressed the idea by saying that such coastal change is very dynamic and that sediments deposited rapidly in one mangrove forest are likely to be eroded and transported from another mangrove stand. Dynamics in sedimentation are likely to deflect any expected or predicted successions in mangrove vegetation. Recently, Zhang *et al.* (2009) described the following pattern of mangrove succession in South China (Figure 2).

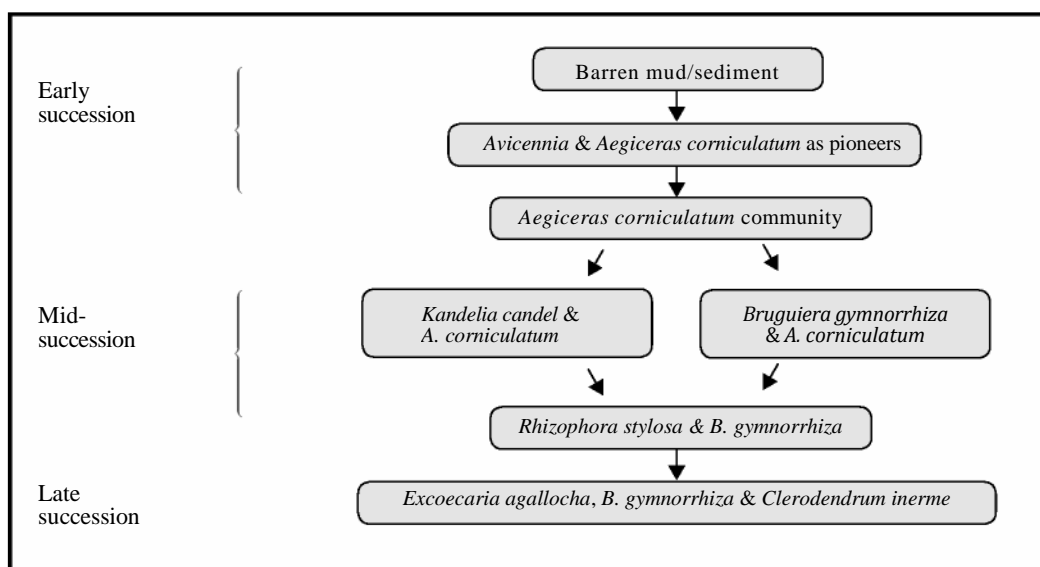


Figure 2 The South China model of mangrove succession (adapted from Zhang *et al.*, 2009)

The principal abiotic environmental parameters that traced this successional sequence were increasing soil salinities and decreasing soil pH. A more recent observation of mangrove succession showed an unusual reversion (Chan, 2014). The expected transition was from the pioneer *Avicennia–Sonneratia* forest to an ecotone of *Rhizophora–Bruguiera* followed by dryland mangrove. In two localities of the Matang mangroves in Malaysia, the dryland mangrove reverted to *Rhizophora–Bruguiera* forest. Forest floor geomorphological changes as surface depression and the consequent inflow of seaward propagules were key factors behind this successional reversal. Chan (2014) considered this reversal of succession to be rare. This may be the case but the atypical nature of this reversal may also reflect the fact that succession is not easy to study due to time constraints imposed by the relative slow pace of succession.

This sort of finding is most important as it tends to support the shifting mosaic concept, quite popular in forest ecology where disturbances (i.e. changes) can serve as regeneration sites that occur episodically and without human impacts (Clark, 1996). Succession is rarely tidy and uniformly a one-way process. The extensive research of Havanond (2000) in Thai mangroves where the mud lobster (*Thalassina anomala*) was an outstanding biotic factor influencing successional dynamics is most relevant here and would add weight to be the shifting mosaic pattern noticed in inland forests (Figure 3).



Figure 3 Mud lobster mounds at Phanga Bay, Thailand (biotic factors in succession dynamics being studied by Ms. Aorrawan of Kasetsart University)

Rovai *et al.* (2012) used the concept of succession in the context of how the planting of the wrong mangrove species in eco-restoration of mangroves can hinder what they called secondary succession in Brazilian mangroves. However, they failed to clarify what primary succession was but argued that mono-specific stands of restored mangrove (human plantation efforts) may compromise the expected normal secondary succession.

A general implication from these rather variable results and research is that rather than being an outdated ecological concept in mangrove science, succession may well provide a useful focus for and hypothesis in mangrove ecology. With the ecological dynamics and variable patterns of mangrove succession in mud-lobster influenced mangrove forests (Havanond, 2000), the notions of secondary succession used by Rovai *et al.* (2012) in the Brazilian mangrove case study may not be the best use of the concept of succession. The mosaics of overlapping stages of succession with patches of vegetation at differing stages representing change like those shown in Figure 2 for China and many other areas at varying stages of progression and reversal being the norm. Indeed, this hypothesis is not new. Ball (1980) captured the idea nicely when she concluded that an intertidal mangrove forest could be envisaged as a mosaic of different successional stages. At most, mangrove science may see both natural and human-induced disturbances to habitats rather than a clear-cut case of succession.

5. Mangrove valuation: Goods and services

Gaps in this important area are many, yet they provide opportunities for seeking funds for research support because any exercise in mangrove valuation becomes an exercise in placing a \$ value on the worth of these natural assets. In short, mangrove valuation is about eco-economics.

5.1 Coastal protection

The December 2004 Indian Ocean tsunami geophysical event did much to stimulate discussion and evaluation of mangrove ecosystems (Aksornkoae, pers. comm.). Despite the powerful evidence in terms of case studies, governmental reports and papers available in Thailand alone, as one of the countries impacted by the tsunami (e.g. Havanond, 2005; Havanond & Maxwell, 2005), some book-sized surveys of ecosystem values have concluded that there is a lack of data on how this protective service arises e.g. Naeem *et al.* (2009). These authors go on to claim that few evaluation studies have used a ‘replacement cost’ method of ‘replacing’ mangroves with human-build alternatives like storm walls. This book is not alone in highlighting the paucity of data on ecosystem values. Barbier (2011) in his attractively titled book, ‘*Capitalizing on Nature, Ecosystems as Natural Assets*’, contended that, ‘there are still a large number of ecosystem goods and services that have yet to be valued or have unreliable valuation estimates’. Later in the book, Barbier (2011) did cite some useful eco-economic valuations in Thailand that demonstrated the positive contribution of mangrove forest stands to coastal protection.

However, from reading the limited literature on mangrove valuations, especially that of coastal protection, one could develop the erroneous notion that all mangrove evaluations are post-2004 tsunami. This is not the case at all. One early pioneer case study was that of Maxwell (1976) who placed a \$ value on the New Zealand mangroves protecting stop banks that protected valuable dairy farmland from storm-driven tidal inundations coinciding with high tide and flooding in low-lying coastal sites due to ‘rain bombs’, which can be climatic features of the Coromandel region of northern New Zealand. Related roles of mangrove vegetation have long been noted and used in Vietnam (Hong & San, 1993). Unfortunately, these New Zealand and Vietnam examples have not been mentioned by the above-mentioned books, thus contributing to a limited awareness of mangrove valuations.

Barbier (2011) created a rather negative perception that mangroves could act as natural barriers against extreme events, such as the Indian Ocean tsunami, when he contended that the evidence was ‘at best mixed’. It is true that tsunamis can deliver huge waves, but some Japanese research presents a very favourable assessment of attenuation of tsunami energy by mangrove forests. Hiraishi & Harada (2003) reported that this attenuation could be up to 90% reduction in maximum tsunami flow pressure for a 100 m wide forest with a tree density of 3,000 stems per ha. In Vietnam, Mazda *et al.* (1997) found that while seedlings of *K. candel* were ineffective in dissipating wave action, trees were able to reduce wave action by 20% over a 100 m distance. Clearly, this topic invites more research and such research may help to reduce the apparent variability in results. Not all mangroves have the same morphology and this fact alone can invite bioengineering and biophysical approaches to determine which tree shape or architecture is best at wave energy dissipation and which species invests more biomass into its above ground root biomass. The potential role of various mangrove species in coastal protection is illustrated in Figure 4.



Extensive prop roots of *Rhizophora apiculata*
(photo by H.T. Chan)



Massive buttresses of *Heritiera littoralis*
(photo by ISME)

Figure 4 Mangrove forests play an important role in coastal protection

Just as there is neglect in this area of mangrove valuation, there remains on-going debate about another outstandingly important question, that of mangroves and fisheries. We will now consider fisheries and conclude with an exciting future prospect, that of the biomedical roles of mangrove extracts and the iconic attraction of tigers and dolphins as enticing topics for mangrove valuation in the future.

5.2 Mangroves and fisheries

Notwithstanding the viewpoint that, there is overwhelming evidence for the role mangroves play in supporting on-site and near-shore fisheries, the direct causal links needed to explain these correlations remain difficult to demonstrate (Macintosh *et al.*, 2013). This lingering uncertainty seems hard to understand when some studies show a strong relationship between fish catches and mangrove-populated waterways (e.g. Pinto, 1987). This positive supportive link between mangroves and fish, shrimp and oyster production has a long history in the Mai Po Marshes of Deep Bay, Hong Kong (Hodgkiss, 1997). Chong's (2007) estimate that mangrove forests sustain more than half of the annual offshore fish landings in Malaysia is in phase with that of Pinto (1987) and Hodgkiss (1997). Another study by Sanchirico & Mumby (2009) showed how mangroves, sea grasses and coral reefs are integrated, and collectively supported the coral reef fish communities. This refreshing work can remind researchers that ecosystems are, themselves, interconnected and that a coordinated study is wise when ecological assessments of coastal ecosystem values and functions are attempted.

Alongi (2009), in perhaps trying to summarize a range of variable information on mangrove and fisheries, felt it apt to be somewhat ambiguous when, on one hand, noting the positive connection between mangrove and shrimp or fish catch, while on the other hand, reporting that we cannot explain the reasons for the connection. He goes on to sum up this situation in a rather humorous way, 'all that can be stated at this time is that estuarine residents, both temporary and permanent, are dependent on mangroves for myriad reasons (known only to the shrimp and fish)'. If we do not know the reasons, then a very eco-economically attractive research topic sits waiting to be addressed.

5.3 Biomedical and bioactive extracts from mangroves

The pharmaceutical values of mangrove extracts remain an understudied area. Some good work was attempted by Thai researchers after the 2004 tsunami (Homhual *et al.*, 2004), but the lingering impression seems to be that the science is limited and that biomedical values of mangroves mostly remain at the folklore level (Saenger, 2002). However, evidence for a reliable biomedical role of a number of mangroves has been noted in an encouraging number of mangrove species (Bunyaphatsara *et al.*, 2003), and including *Barringtonia asiatica* (Khan & Omoloso, 2002), *Hibiscus tiliaceus* (Maganha *et al.*, 2010) and *R. stylosa* (Kainuma *et al.*, 2015). Hong & San (1993) listed eleven species of mangroves as sources of local medicine in Vietnam, but the biomedical basis for these claims are unknown.

Thangam & Kathiresan (1992) reported that some mangrove plant extracts exhibited mosquito larvicidal activity against *Aedes aegypti*. Maxwell (1971) observed that tannin-polyphenols exuded from mangrove (*A. marina* var. *resinifera*) leaves and seedlings inhibited the maturation of *Culex* mosquitoes. These insecticidal properties of mangrove extracts present an attractive line of inquiry. Recently, Chan *et al.* (2012a, 2012b) showed that wood vinegar from the Matang mangroves displayed potent antibacterial, antioxidant and skin-whitening activities. Collectively, while limited in scope to date, these findings indicate that investigations of bioactive properties of mangrove extracts merit much more research. Such research may well focus on biomedicines but also consider questions in the field of chemical ecology, e.g. do leaf leachates of mangroves inhibit rooting in mangrove seedlings (Kathiresan & Thangam, 1989).

Answers to questions such as this may help us to more fully explain why there seems to be such a poor understorey in most mangrove forests (Janzen, 1985; Snedaker & Lahmann, 1988) with candidates for the niche of an understorey species being rare. *Brownlowia tersa* is such a shrub in the pristine mangroves of Brunei (Maxwell & Havanond, 1991) and the mangrove fern, *Acrostichum* spp. approximates an understorey herb (Saenger, 2002), but may also indicate habitat disturbance such as semi-open spaces near dead trees or on the higher ground associated with mud-lobster mounds (Figure 5) (Maxwell & Havanond, 1991; Aksornkoae *et al.*, 1992).

*Acrostichum aureum*

Photos by H.T. Chan

*Acrostichum speciosum***Figure 5** Thickets of *Acrostichum* ferns growing on exposed higher ground in association with mud-lobster mounds

5.4 Tigers and dolphins

Both the Bengal tiger (*Panthera tigris tigris*) and the Sumatran tiger (*Panthera tigris sumatrae*) are listed as endangered, with the Sumatran subspecies as critically endangered (IUCN, 2012). The role of the Bengal tiger in the Sundarbans, the largest continuous tract of mangrove forest in the world (Saenger, 2002) as having the spotted deer as its principal prey is well known. What is unknown is its possible status as a keystone species within this massive mangrove ecosystem. Just how does the presence of wild tiger populations control food web dynamics? Would its demise have a major impact on the ecological economy of the 10,000 km² mangrove forest that make up the Sundarbans? Similar questions should be asked for the Sumatran tiger.

Recently, Maxwell & Lai (2012a) advocated that the Irrawaddy dolphin (*Orcaella brevirostris*) should be elevated to the status of an iconic species in trans-boundary plans aimed at ecological repair and conservation of coastal ecosystems. As with the tiger case, research that would illuminate the role and status of dolphins such as *O. brevirostris* in these estuarine mangrove ecosystems would be most welcome. Indeed, both the Bengal tiger and Irrawaddy dolphin have the potential to become icons like the charismatic panda.

5.5 Mangroves as food

Hong & San (1993) recorded that several species of mangrove provided food for coastal communities in Vietnam, especially during times of famine and war. Field (1995) extended this knowledge and even provided a recipe for cooking the propagules of *A. marina*. Beyond human food needs, mangroves have been used as fodder for cattle (in Vietnam and the Middle East) and goats (in Vietnam). Hong & Tuan (1981) showed that the fruits (propagules) and leaves of *A. marina* were the preferred parts by cattle. The palatability and high protein content contributed to this foraging preference. Maxwell & Lai (2012b) showed that *A. marina* foliage and twigs were selectively foraged by dairy cattle on a New Zealand farm and suggested that the eco-economic status of the New Zealand mangrove resources could be enhanced if a dollar value was placed on this food as a sustainable salt rich nutrient. Such a demonstration would do something to banish the negative perception towards mangroves that has developed in some sectors of New Zealand society in recent years. Recently, Baba *et al.* (2013) provided a comprehensive account of mangroves as food for humans, and as fodder and forage for livestock in their book *Useful Products from Mangrove and other Coastal Plants*.

5.6 Mangrove valuations: Urgently needed

The contributions made by mangrove ecosystems to coastal protection and fisheries together with a demonstrated potential as a bank of bioactive and biomedically valuable compounds are in themselves worthy of comprehensive eco-economic valuation studies. If we add the enticing roles of mangrove products and resources as food for humans and domestic animals to these considerations, then valuations take on a new dimension. A dimension in which they become too good to destroy – for destroying, degrading or damaging such ecological resources would represent economic madness. The place of both the tiger and Irrawaddy dolphin in the world's biggest mangrove resource have the potential to promote, to market, and to sell the compelling notion that mangrove resources are just too valuable to destroy or damage. The report of Macintosh *et al.* (2013) clearly demonstrated, in the strongest of scientific, sociological, political and economic terms, that mangrove conservation, rehabilitation and even improvement (more

biodiversity in plantations) are excellent investments. Applied in a trans-boundary way, the benefits can help to unify national efforts in a shared ecosystem.

6. Applied science: Eco-restoration and heavy metal capture

Eco-restoration can be viewed as the ‘acid test’ of ecology (Bradshaw, 1990). Projects designated as eco-restoration have been around for a long time. For example, village-based mangrove restoration schemes in the Philippines have a 50-year history (Walters, 2003). However, the recent TBDA project (Macintosh *et al.*, 2013) revealed that too many so-called restoration projects fell short of the essential scientific ecology input to ensure their success. Not only are eco-restoration schemes challenging ecologically, to conduct them correctly can be a costly exercise. Barbier (2011) calculated that the full cost of replanting and restoring mangroves in abandoned shrimp ponds for the entire capitalized value of the restored services. His estimate totalled \$12,392 per ha! In my view, this is an extreme case where economic and financial accounting may have dominated the thinking. Research opportunities in this area exist and the initial focus should be on the correct choice of mangrove species to match the site under study. Community participation, monitoring, at least partial ownership and profit-sharing from the activity together with input from professional ecologists and foresters can greatly contribute to success in eco-restoration schemes (Macintosh *et al.*, 2013).

6.1 Mangrove as sinks for industrial waste containing heavy metals

Some studies indicate that mangroves may be able to cope with heavy metals (HM) at modest concentrations and even capture and hold them in mangrove root rhizosphere (Lacerda *et al.*, 2000). Species include *R. mangle* (Machado *et al.*, 2004), *A. alba*, *A. marina*, *A. corniculatum*, *K. candel* and *R. mucronata* (Wong *et al.*, 1997). One study found that Cu and Zn, accumulated in the roots with limited translocation to the leaves (Tam & Wong, 1997), but another similar study showed that, in contrast, metals do reach the leaves of *A. marina*, especially Zn and Cu, and with the root epidermis providing a barrier to the transport of lead (MacFarlane & Burchett, 2000). Moreover, these metals could be extruded from the glandular trichomes on *A. marina* leaves. The implications of this limited research are that much more field-based investigation on the ecotoxicology and biology of mangroves and HM is desired and urgently needed before mangrove stands are deemed suitable as sites for the discharge of wastes. One outstandingly important consideration that has been ignored by those advocating using mangroves as pollution and landfill management tools is the disposal of the ecotoxic materials. Should it be convincingly shown that mangroves can sequester HM, then can the desired post-sequestration technology harvest these HM? In short, can they be re-cycled in an environmentally safe and scientifically sound manner? Questions such as these in mangrove science, invite multi-disciplinary approaches to problem solving and research design. In today’s world, such approaches have enhanced chances of attracting funding.

6.2 How much biodiversity is necessary to maintain full ecosystem functionality?

Questions such as this are becoming increasingly relevant as natural ecosystems become harder and harder to find. Ecologists have for many years raised issues such as conservation programs should focus on ecological processes rather than simply saving species (e.g. Smith *et al.*, 1998); biological integrity is more important ecologically than biodiversity (Angermier & Karr, 1994); and how much biodiversity is needed to maintain ecosystem functions (Risser, 1995)

These issues and questions are as relevant today as they were two decades ago. Indeed, when one surveys the mangrove ecosystems of the world one can find low biodiversity uni-specific stands of mangrove that can nevertheless support rich fisheries. This was the case in Brunei with an almost uni-specific stand of *A. marina* (Maxwell, 1991, 2015) and in New Zealand (pers. obs.), again with *A. marina*. The question of how much biodiversity was needed to sustain ecosystem functionality and provide a good range of ecosystem goods and services was again a hot topic at the TBDA workshop (Macintosh *et al.*, 2013). This topic, when applied to mangroves, offers much in the way of research opportunities and recent discussions with the Director of the Mangrove Forest Research Centre at Ranong, southern Thailand (Dr. Meepol) support this opportunity.

In terms of mangrove eco-restoration methods, there is still much room for investigation and improvement. Recent restoration activities led by NGOs with local community involvement have shown that the removal of dead mangroves is *not* a desirable pre-condition before restoration (Primavera *et al.*, 2012). It has been shown that such action is unwise ecologically and should be avoided. The core reason for this is that the dead mangrove biomass is a habitat and has important below ground biomass and that such material is part of the nutrient biogeochemical cycling,

and although work in this important dimension of mangrove ecosystem function is very limited. Boto (1991) has shown that most soil N and P is contained in organic forms and the little organic P that is present is bound within hydrated ion and aluminium oxyhydrates, severely limiting its availability to plants (Saenger, 2002, citing Boto, 1991). Leaving this non-living biomass in the soil provides opportunities for microbially assisted biogeochemical nutrient re-cycling and mobilization. The same eco-hydrology group (Primavera *et al.*, 2012) also advocated that eco-restoration should be as natural as possible. This means allowing the remaining post-storm (typhoon) surviving mangroves to do their own eco-repair.

7. Language of mangrove science

In this short but important section, the variable language that is sometimes applied to the same ecological concept is briefly examined. Such an examination may appear to be out-of-place here and at home in journal of linguistics, but in my hard-won assessment, this is not the case at all. Alternative terms for the same or closely related concept are quite frequently encountered in the mangrove literature. Here only a few will be mentioned in an effort to illustrate the point.

'True' vs. 'associate' mangrove or 'exclusive' vs. 'non-exclusive' are semantic variations linked to both the history and sociology of mangrove science. The 'true' vs. 'associate' dichotomy has its origins in the first few decades of the 20th Century. The terms have endured because they provide some convenient descriptors. To many mangrove ecologists 'true' mangroves are visited by normal high tides on a regular basis as is typical of the intertidal zone (littoral zone). 'Associate', on the other hand, may only experience a limited and partial tidal inundation, sometimes restricted to extreme high tides. Nevertheless, the salt water brings salt and this salt factor remains in the soil even when the tide retreats and the water evaporates. For this reason, it can be unscientific to assume that the soils in which these more 'back' mangroves live are less salty than those that receive regular tidal inundation. A case could be made to replace the term 'true' mangroves with 'exclusive' mangroves and extend the thinking to cover 'associate' or 'non-exclusive' species. It is also tempting to advocate that 'associates' be called ecotonal species. However, all these semantic gymnastics will remain rather academic until we have a solid, robust scientific basis in the eco-physiology of all mangroves i.e. the so-called 'true' and 'associates'. It is on the cards, that some of the species that are mostly found in the 'back' mangroves, are there because they are less competitive than those 'exclusive' species when faced with the physiological demands of growth, survival and competitive reproductive success in the sometimes anoxic and consistently hyper-saline substrata that can be found in the more tidal reaches of the mangrove zone. In short, such 'associates' may well be salt tolerant and therefore 'true' halophytes but not as competitive as their better-adapted counter parts. When extreme events, such as geophysical tsunamis, bring a landward invasion of seawater many meters above extreme high water marks, terrestrial trees die as do many grasses and other land plants. The so-called back mangroves, in contrast, can cope with such saltwater insult.

Carbon balance or allocation is very similar in linguistic terms and both have been applied to identical ideas, i.e. where different mangroves put their carbon-based biomass. Does the term production mean carbon fixation by photosynthesis? Does it mean carbon capture by photosynthesis? It can mean both. The term is also used in a way that means the process of generating new biomass. Sometimes the output, rather than the process, is termed productivity. Ecological restoration can mean various approaches to mangrove ecosystem repair such as rehabilitation and re-plantation of one or just one or two available mangrove species. Typically, the term does not mean ecosystem restoration, which would be an impossible task in practice. The term needs attention.

8. Concluding thoughts

Is there a candidate conclusion arising from this review of gaps in mangrove science? I propose that there is such a conclusion and perhaps this is most appropriately expressed as a paradigm for mangrove science suitable for the next two or three decades of the 21st Century. The number of pristine mangrove stands remaining is few. For this reason alone, we could advocate that the best paradigm for mangrove science today would be that of mangrove eco-restoration. I strongly subscribe to the argument expressed by Bradshaw (1990) that restoration is the acid test of ecology. Mangrove ecosystems in their non-pristine form are the norm globally. The TBDA workshop made this fact abundantly clear. Thus, in terms of where most mangroves are throughout the world and the attendant challenges to restore and to re-build mangrove ecosystems where they make eco-economic sense, a paradigm of eco-restoration is more than just relevant. It is a necessity. The famous Matang mangroves in Malaysia with over 100 years of sustainable use provides a model of how an eco-economically sound mangrove can be managed scientifically. An impressive literature records the history of Matang's enduring success (Watson, 1928; Dixon, 1959; Ong, 1982; Saenger, 2002; Muda & Mustafa, 2003; Chan, 2014).

An eco-restoration paradigm can provide the sort of emphasis and focus to bringing new life to the many gaps in mangrove science and, at the same time, test the depth of our existing bank of knowledge. The age of pioneering discoveries that were once easy to make when natural mangrove ecosystems were the norm is over. Today the relatively few remaining stands of natural mangrove are out-numbered by the human-impacted mangrove ecosystems in various stages of ecological ill health. The time for eco-restoration is upon us.

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