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Functional Diversity in the Hyper-diverse Mangrove Communities in Papua New Guinea

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I am submitting herewith a dissertation written by Lawong Balun entitled "Functional Diversity in the Hyper-diverse Mangrove Communities in Papua New Guinea." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Taylor Feild, Major Professor

We have read this dissertation and recommend its acceptance:

Edward Shilling, Joe Williams, Stan Wulschleger

Accepted for the Council:
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(Original signatures are on file with official student records.)

Functional Diversity in Hyper-diverse Mangrove Communities in Papua New Guinea

A Dissertation Presented

For the Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Lawong Balun

December 2011

DEDICATION

To my father, mother, father in law, mother in law

Balun Garap, Marawe Garap, Lalai Kulang Yam, and Nang Gamun Yam

and my wife

Laden Kulang Balun

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ABSTRACT

Variation in plant functional traits reflect the differences in an environment a species occupies and the variation in the functional traits across an environmental gradient and growth form reflects the functional performance of the coexisting species. Therefore, detecting the differences in functional traits of species is important to our understanding of the performance of species. The leaf functional traits; Leaf mass per area (LMA) and vein density (D_V) are key traits in the resource use strategies and photosynthetic gas exchange capacity (A_{max}, g_{smax}) of all plants. Mangroves occupy a hypersaline narrow ecological range and therefore are thought to have uniform functional performance. This view makes sense for low diversity mangrove communities, but what about the hyperdiversity communities such as those in New Guinea? A comprehensive review of the present understanding on the ecology and socio-ecological values of mangrove was undertaken to establish a good foundational understanding of my study on New Guinea mangroves (Chapter 1). It is widely held that mangroves thriving in a hypersaline environment experience high water constraints and as a result have high water use efficiency, therefore have narrow functional performance. I investigated the leaf and photosynthetic functional traits of 31 mangrove species among different zonation bands and growth from six mangrove communities in New Guinea to test the view that mangroves have a narrow functional performance (Chapter 2). I then investigated the differences in wood and stem hydraulic traits among different zonation bands and growth forms and the relationship between wood hydraulics and leaf photosynthetic gas assimilation functional performance to further test the long standing view that mangroves have a narrow functional performance (Chapter 3). I then summarized the major findings of my two studies and their implications

on mangrove restoration and rehabilitation with particular reference to the recent mangrove rehabilitation initiatives in Papua New Guinea (Chapter 4). My studies on leaf and wood functional traits across different zonation bands, growth forms and root system types consistently revealed that mangroves have a wide functional performance, and different species exhibited different resource use strategies.

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CHAPTER I: MANGROVE AND MANGROVE FOREST

INTRODUCTION

Mangroves are plant communities comprising a wide range of unrelated taxa, which grow at the interface between the marine and terrestrial ecosystems (Tomlinson 1986). Mangroves are specialists of low tidal-energy, saline, anoxic soils, and low nutrient sedimentary shorelines and inter-tidal areas and river deltas of tropical and subtropical latitudes (Stewart and Popp 1987). The majority of mangroves are widely believed to exhibit striking evolutionary convergence in their overall functional and morphological characteristics (Lugo and Snedekar 1974, Tomlinson 1986; Ball 1996, Sobrado and Ball 1999, Naidoo *et al*. 2002). For example, mangrove species have evolved similar functional, ecological, and morphological characteristics, such as aerial roots, succulent and glossy leaves with thick cuticles, leaf inclination greater than a 90^o angle, and viviparous reproduction (Tomlinson 1986). Mangrove species rarely occur outside intertidal areas, and they mostly occur between mean sea level and the mean level of high water spring tides (Lear and Turner 1977, Belperio 1979).

In textbooks, the term “mangal” is used interchangeably with the mangrove vegetation or ecosystem (Robert *et al*. 2009). The brackish zone of the mangal system in regions of low topographic relief such as tropical flood plains can penetrate inland into riverine communities. Thus, mangal systems are often broadly defined as woody vegetation types occurring in marine and brackish environments (Hogarth 1999). The mangal system in its broadest sense includes the “*Nypa* formation”, a coastal vegetation type dominated by the rhizomatous palm, *Nypa fruticans,* commonly associated with the estuarine-river delta mangrove system, and margins of mangroves that are inundated a few times a year during spring tides and storm surges. It also frequently includes species from adjacent vegetation types such as the beach "*Barringtonia*" formation- a coastal vegetation type with woody species predominated by *Barringtonia* spp and sand dune *"Pes-carprae"* formation-a coastal beach sand dunes covered by creepers, in which *Ipomoea pes-carprae* (Convolvulaceae) dominates (van Steenis 1958, Macnae 1968, Tomlinson 1986).

Interest in mangroves has recently heightened in recognition of the important roles that these forests play in the following: coastal primary productivity (Mitsch and Gosselink 2000, Lovelock *et al*. 2004, Kraus *et al*. 2006, Barr *et al*. 2009); carbon storage (Twittley *et al*. 1992, Smith *et al*. 1994, Alongi 2008, Bouillon *et al*. 2008, Donato *et al*. 2011); and key roles in coastal biogeochemical cycles (Robertson and Alongi 1992, Bouillon *et al*. 2008). Despite recognition of the global significance of mangrove ecosystems, mangrove primary productivity, carbon storage potential, and the feedbacks of these processes on coastal biogeochemical processes remain poorly studied. A comparative study on the plant-based parameters, such as leaf photosynthetic carbon-water use, that influence the above aspects of mangrove communities is important in improving our understanding of the functional performance of mangroves and their key roles in global biogeochemical processes. My Ph.D. research on six hyperdiverse mangrove communities in Papua New Guinea (PNG) focuses on understanding the patterns in the ecological and physiological processes responsible for maintaining the community dynamics, in particular productivity, growth, and survival. The fundamental plant-based data on how mangroves function will be of broad interest to workers in disparate areas of mangrove biology in shedding new light on how mangroves: (1) photosynthesize and regulate water-use; and (2) how high diversity mangrove communities differ in their ecological strategies.

Mangrove forests are widely considered to be a highly productive but widely threatened tropical coastal ecosystem. It is estimated that mangrove forests sequestrate $218 \pm 72 \times 10^9$ kg C a^{-1} (Bouillon *et al*. 2008a) to 1,023,000 kg C $ha^{-1}yr^{-1}$ (Donato *et al*. 2011) and contribute ~10% of the global particulate and dissolved organic carbon to coastal ecosystems (Dittmar *et al* 2006). However, the areal extent of mangrove has declined by 30-50% over the last 50 years due to anthropogenic land-use change (Valiela *et al.* 2001, Donato *et al*. 2011). Regional and local studies on plant functional traits suggest that plants are limited in their physiological solutions to environmental stresses; hence, plants in similar environments may exhibit similar functional and physiological performances (Reich *et al*. 1997, Pareulo *et al*. 1998, Meinzer 2001, 2003, Reich *et al*. 2003, Bucci *et al*. 2004). There are some data on mangrove productivity (Ball and Farquhar 1984a, b, Twilley *et al*. 1992, Snedaker and Araújo 1998, Sobrado 2000, Barr *et al*. 2009, Donato *et al*. 2011), however, most of these data are from high latitude, low diversity mangal systems. Therefore, all previous studies are inadequate as an answer to the above question in a broad manner. Inclusion of photosynthetic performance measurements, which are the ultimate drivers of primary productivity, from low latitude, high diversity mangrove ecosystems are critical to understanding the ecological and physiological performance of global mangrove ecosystems. Additionally, knowledge of patterns in functional traits of plants from hyperdiverse mangrove communities in PNG should provide data necessary for making broad predictions on productivity, growth, and sustainability of global mangrove communities. Such data are also essential for any future efforts to restore degraded mangrove forests (Gilman *et al*. 2006).

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My PhD research examines the functional performance of six hyperdiverse mangrove communities in PNG and makes comparisons of the leaf and wood functional traits across the different biogeochemical environmental gradients (zonation) and growth forms. **My a priori hypothesis is that the hyperdiverse mangrove communities in PNG exhibit a narrow functional performance despite their wide phylogenetic diversity.** Before outlining the motivating logic behind my hypothesis, I first provide a comprehensive review on present perspectives on the function of mangrove ecosystems in a global context and then focus on the key importance that studies on New Guinean mangrove forests can contribute in addressing global-scale questions surrounding mangrove forest function. I will therefore in the subsequent discussion review the current perspectives on the following topics: global distribution and diversity, New Guinea mangroves, ecology of mangrove, evolution of mangrove, then conclude with my dissertation focus. I will pay particular attention to the ecology of mangrove in view of the functional attributes associated with zonation, succession, salt excretion, and rooting structure.

Mangrove global distribution and diversity

Mangroves are distributed throughout the coastlines of the world's tropical and subtropical regions. They originally (30-50 ma, Duke 1995) covered 75% (20 million ha) of tropical and subtropical coastal regions (Tomlinson 1986) but have been reduced to 15.2 million ha globally over the last century (Groombridge 1992, FAO 2007). Mangroves account for ~30-35% of the global area of tropical wetland forest (FAO 2007, Giri *et al*. 2011, Page *et al*. 2011). Mangroves generally grow between 25^{o}N and 25^{o}S latitude, with outliers occurring farther south in New Zealand (34^{o}S; 173^{o}E), and farthest north in Japan (32^{o}N; 131^{o}E) (Choudhury 1996). The most extensive mangrove communities currently occur in the following geographical regions: New Guinea, the Ganges and Brahmaputra deltas in India, Bangladesh, the coast of Sumatra and Borneo (Indonesia), Australia's Queensland and Northern Territories, and both the east and west coasts of tropical and subtropical Africa and tropical America.

There are a variety of global estimates for mangrove plant diversity, but conservative estimates are from 80 (60 true + 20 associates) to 114 associated species of trees and shrubs (Saenger *et al*. 1983, Tomlinson 1986, Duke 1992, Ellison *et al.* 1999). Floristic analyses of mangroves show two, biogeographically distinct regional groups: the Indo-West Pacific (IWP), which comprises Asia, Australia, Oceania, and the eastern coast of Africa; and the Atlantic-Caribbean East Pacific region (ACEP), which covers the Americas and the western coast of Africa (Duke 1992). It is hypothesized that the cold water at the southern tip of Africa and the large distance between Asia and America divide the two regions (Tomlinson 1986, Duke 1995). The two mangrove regions cover a similar total area but vary floristically. Local mangrove diversity in the ACEP region is generally 3-4 species in a community, whereas the per-community diversity in the IWP is 11-33 (Macnae 1968, Chapman 1976, Bunt *et al*. 1991, Ellison and Farnsworth 1997, Duke *et al*. 1998). This pattern of diversity observed in the two regions is termed "the mangrove diversity anomaly" (Ricklefs and Latham 1993). Diversity in mangroves varies among geographical regions; some communities constituting only one or two species (e.g. those in the Red Sea in the Mediterranean) whereas others such as those in New Guinea have 30 - 47 species (FAO-UNEP 1981, Ellison and Farnsworth 1997, Duke *et al*. 1998).

It is estimated that 30-50% of the world's mangrove forest have been lost in the last half a century (Valiela *et al*. 2001, Alongi 2002, Duke *et al*. 2007, FAO 2007, Polidoro *et al*. 2010, Danota *et al*. 2011). Mangrove deforestation comes from conversion of natural stands into aquaculture, as well as timber harvesting, land reclamation, urbanization, and rising sea levels (Valiela *et al*. 2001). The speed at which the global mangal system is disappearing poses a major threat to its sustainability and the overall degradation of estuarine areas (FAO-UNEP 1981, FAO-UNEP 1985, Spalding *et al.* 1997, Barr *et al*. 2009, Loarie *et al.* 2009). Mangal loss is a global concern because mangrove deforestation is occurring at a rate of 2.1% per year in almost all the countries that have mangroves (Valiela *et al*. 2001). In fact, mangroves are threatened with extinction in 26 out of the 120 countries having mangroves (FAO 2003). The rates are rising rapidly in developing countries, including PNG where more than 90% of the world’s mangrove diversity is located. The losses in functional diversity of mangrove forests due to deforestation pose a threat of species’ extinction (Duke *et al*. 2007).

The global significance of mangrove forests

Mangroves are a key habitat for important global ecological and biogeochemical functions, including shoreline protection, sediment accretion through trapping and accumulating silts, retarding the erosive impact of tsunami, storm and cyclone surges, filtering suspended particulate matter and debris from terrestrial runoff and floods, and maintaining the carbon balance of tropical coastal ecosystems (Field 1995, Dittmar *et al*. 2006, Vermaat and Thampanya 2006, Bouillon *et al.* 2008b, Das and Vincent 2009). Overall, water flowing through the mangrove ecosystem is cleaner and of better quality than the flood waters flowing directly into the coastal marine ecosystems such as coral reef ecosystems.

Mangrove ecosystems are major sources of primary productivity that drives the complex food chain that supports many terrestrial and marine organisms. Additionally, mangrove forests provide foraging and roosting sites for bats, birds, and arboreal mammals (Baran and Hambrey 1998, Barbier 2000). Mangrove plants often possess dense and intricate rooting networks that capture effluents from terrestrial runoffs of domestic and industrial pollutants. These root systems may also act as a biological sink in sequestrating atmospheric carbon, thereby reducing global carbon dioxide levels and biogeochemical cycles. More recently, mangroves have been proposed as a biological indicator for understanding and predicting changes in coastal environments derived from global climate change (Dittmar *et al*. 2006, Bouillon *et al*. 2008a).

Mangrove ecosystems are considered to be among the most efficient tropical coastal ecosystems in primary production with an estimated biomass of 28.2 kg m^{-2} (Briggs 1977), 23.6 kg m^{-2} (Clough and Attiwill 1975), ~30-40% of terrestrial Net Primary Productivity (NPP) (Malhi and Grace 2000), and ~218±72 Tg C yr^{-1} (Bouillon *et al*. 2008a). For example, NPP in mangroves ecosystem is 7 to 11-fold greater than the tropical rain forest. Primary productivity is expressed as the gross primary productivity minus the losses in respiration and herbivory (Whittaker *et al*. 1975). Primary productivity can be measured as above-ground net primary production through a measure of biomass increments, and can be assayed in part using infrared gas exchange measurements to determine photosynthetic CO_2 assimilation rates (Malhi and Grace 2000, Keith *et al*. 2009, Page *et al*. 2011).

Estimates of various carbon sinks (organic carbon export, sediment burial, and mineralization) indicate that over 50% of the carbon fixed by mangroves is unaccounted for (Bouillon *et al.* 2008b). Losses in biomass that occur due to leaf, stem, and root respiration account for 4-10% of the primary productivity (Lugo *et al.* 1975). These losses are often considered insignificant. However, Clough and Attiwill (1975) argued that these losses could be much higher than what Lugo and colleagues estimated. This high-energy material (mangrove biomass) makes a substantial contribution to the estuarine and inshore productivity via a complex food chain (Heald 1960, Odum 1971), and has a potentially high impact on the global tropical carbon budget (Bouillon *et al*. 2007). Limited studies on mangrove biomass indicate that mangroves have a high root/shoot ratio (Clough and Attiwill 1975, Briggs 1977). The high root biomass in mangroves implies that the below ground biomass in mangrove potentially play an important role in the biogeochemical cycle.

Mangrove forests exert a strong influence on coastal geomorphology, and make a key contribution to carbon biogeochemistry (Twilley *et al*. 1992) and carbon cycle in coastal seawater (mineralization, burial of organic carbon, carbonate production and accumulation that take place in the coastal ocean; Gattuso *et al*. 1998, Mackenzie *et al*. 2004, Duarte *et al*. 2005). A recent study indeed indicated mangroves are among the most carbon-rich forests on the planet with primary productivity rate of ~1,023,000 kg C $ha^{-1}yr^{-1}$ and that they bury between 48-98% of carbon in their peat soil (Donato *et al*. 2011). This suggest that ~2% of carbon fixed in the mangrove ecosystem is unaccounted for in contrast to the earlier study (Bouillon *et al*. 2008b), who claimed more than 50% of carbon fixed in mangrove ecosystem are unaccounted for. Mangrove ecosystem sequestrates 7 to 11-fold greater carbon than tropical rain forest ecosystem (15.6×10^5 kg C $ha^{-1}yr^{-1}$; Malhi and Grace 2000 and 90,000 kg C $ha^{-1}yr^{-1}$, Iverson *et al*. 1993) sequestrated by tropical rain forest ecosystem, 18-fold and 24-fold greater than temperate forest (56,042 kg C $ha^{-1}yr^{-1}$) and other wetlands (42,592 kg C $ha^{-1}yr^{-1}$) respectively (Gorte 2009). Mangroves develop a unique extensive root architecture that serves as a buffer to erosive forces that batter the coastlines. By dissipating hydrodynamic energy, they promote sediment deposition and sediment accretion through trapping and accumulating silts and other terrestrial organic debris. Mangrove forests also function as a natural filter of suspended particulate matter and debris from terrestrial runoff and floods. The extensive aerial root system of mangal forests filters flood waters and other terrestrial runoffs from heavy suspended organic matter and debris and provides the adjacent coastal marine system with sediment-free water (Robertson and Philip 1995, Rivera-Monray *et al*. 1999). Mangrove water filtration indirectly protects and promotes coral reef and sea grass communities from potential death because of increased sedimentation (Choudary 1996). The extensive aerial rooting structures also serve as a net for capturing effluents from terrestrial runoffs transporting domestic and industrial pollutants (Duke 1995).

The root structure and architecture of mangrove ecosystem are critical components in the trapping and cycling of organic material, chemical elements, nutrients and storage of the riverine material fluxes. Those in the tropics alone deliver 50-70% of all riverine sedimentary debris, terrestrial carbon, and runoff to the oceans (Milliman and Meade 1983, Milliman and Syvitski 1992, Meybeck 1988, Ludwig *et al*. 1996, Richey 2004). High relief islands of the Indo-Pacific archipelago, such as New Guinea, supply roughly half of the tropical inputs worldwide (Milliman and Syvitski 1992, Milliman *et al*. 1999). Benthic and pelagic communities within these ecosystems interact with and reflect physical conditions over a variety of time scales (Alongi 1998).

With respect to sedimentation processes, the distribution, abundances, and activities of organisms are often strongly impacted by episodic or periodic physical events, such as water column turnover, sediment suspension, and organic matter deposition (Alongi 1995, Aller and Stupekoff 1996, Aller and Todorov 1997). One study on mangrove restoration sites and mixed basin forests (McKee and Faulkner, 2000) demonstrated that biogeochemical functioning of restored mangrove forests depended on a number of factors. Local and regional factors such as the saline regime act together with the site's history to control primary production and turnover rates of organic matter in restoration sites. The production of organic matter, establishment of food webs, movement of carbon, energy, and recycling of nutrients are important functional aspects of mangrove ecosystems (McKee and Faulkner 2000).

Mangroves' ability to occupy and reproduce successfully in a highly unstable and overly inundated environment is achieved through structural modification of the rooting system as well as vivipary (when seeds germinate while still attached to the parent plant). For example, members of the family Rhizophoraceae (e.g., *Rhizophora*, *Bruguiera*, and *Ceriops*), which daily experience the dislodging stresses of wind, sea waves, tidal fluctuations, frequent storm surges, and tsunamis, have evolved adventitious or aerial roots such as stilt and prop roots which provide mechanical stability and allow vivipary reproduction to increase survivorship. *Rhizophora* aerial roots typically emerge horizontally from the main stem ~3 m above the ground and prop downward at ~45^{o} away from the stem to anchor in the soft muddy substrate (Fig.1.1). Other species such as those of *Xylocarpus* and *Heritiera* evolved plank buttresses (modified flattened stilt roots that are joined to the stem to base (Fig.1.2), which extend away from the main trunk in a sinuous manner on soft, loose substrate to attain mechanical stability (Floyd 1977). The highly inundated soil environment of mangroves deprives the plants of oxygen;

hence, aerial roots also act as functional breathing roots for intake of oxygen through lenticels. Other species (*Avicennia* species and *Sonneratia* species), which do not possess pronounced aerial roots, have evolved pneumatophores (Fig.1.3) and knee-like roots (Fig.1.4; vertical outgrowths projecting above the surface from the horizontal roots just below the level of the soft substrate) for aeration (Floyd 1977, Tomlinson 1986).

Mangrove fruit vivipary (seeds within fruit germinating while still attached to the parent tree) is an adaptation for rapid establishment in the tidal zone where wave and daily tidal actions are unavoidable. For example, fruits of members of family Rhizophoraceae and Myrsinaceae (*Aegiceras*) germinate while still attached to the parent tree so that when they fall to the ground, or are washed up on a suitable substrate; roots are quickly produced to anchor the young plant against the action of the tides (Floyd 1977, Tomlinson 1986).

Figure 1.1. Prop and stilt roots of *Rhizophora stylosa* (Rhizophoraceae) propping in a soft muddy substrate (Riwo mangrove, Madang Province, PNG).

Figure 1.2. Sinuous plank buttress roots of *Xylocarpus granatum* in a soft muddy substrate (Labu mangrove, Morobe Province, PNG).

Figure 1.3. Pneumatophore (breathing roots) of *Sonneratia alba* (Sonneratiaceae) extending above water in a soft muddy substrate (Wangang mangrove, Morobe Province, PNG).

Figure 1.4. Knee-like roots of *Bruguiera sexangula* in the central mangrove zone (Wangang mangrove, Morobe Province, PNG).

New Guinea mangroves

The name New Guinea and Papua New Guinea (PNG) are used interchangeably in scientific literature (van Steenis 1958, Gressitt 1978, Paijmans *et al.* 1976, Beehler *et al.* 1986), where the latter demarcates a political boundary between the Indonesian province in the western half of the island and an independent state of PNG to the east and the former represents the island land mass. Because biota of the island of New Guinea are not demarcated by human political boundaries, including mangrove ecosystem I will used both names interchangeably in my dissertation research.

Of the major global centers of mangal forest diversity and abundance, the island of New Guinea has one of the largest (~3,443,000-4,100,000 ha) (Duke 1992) areas of well-developed, species diverse (47 species) mangrove ecosystems in the world (Ellison and Farnsworth 1997, Duke *et al.* 1998). New Guinea's mangal system includes about 83% of Southeast Asia (SEA) and 78% of the world's mangrove species. The largest contiguous area of mangroves in New Guinea lies in the Kikori and Purari mangal systems of the Gulf of Papua and covers an area of ~260,822 ha (Shearman 2010).

The zonation of New Guinea's mangrove communities is similar to that of the rest of SEA, ranging from three to five zones. The most well-developed mangrove stands in New Guinea have an average canopy height of 30 m, growing to one m stem diameter at breast height (dbh) in *Xylocarpus granatum* (FAO-UNEP 1981; L. Balun, personal observations 2010). Mangrove forests in the low topographic relief floodplains in the southern part of New Guinea (Kikori and Daru) penetrate the riverine habitat for a considerable distance inland with the furthest inland mangrove forest located 300 km up the Fly River in Western province (Percival and Womersley 1975).

Mangrove communities in New Guinea are dynamic and highly sensitive to soil and water salinity, drainage, and inundation periods (Alongi *et al*. 1992, Harris *et al.* 1996, Harris *et al*. 2004, Shearman 2010). Mangrove species' zonation within the intertidal area reflects a successional process attributed to the aforementioned factors (Cragg 1983). Recent studies in the Gulf of Papua revealed substantial changes in local mangrove distribution over the last 34 years, caused by changes in seaward progradation (land building or sediment accretion) of the Purari Delta and the regression (land disappearance) of the Kikori Delta by an average of 43 m per year at its most seaward point (Shearman 2010). These changes were speculated to be a continuation of long-term trends, which involve interactions of factors such as rising sea level, climate change, and changes in sediment dynamics (Shearman 2010). Mangroves also undergo spatial modification and succession due to the dynamic environment. For example, in calm, open coastal shorelines, species with the highest salinity tolerance such as *Aegialitis annulata*, *Avicennia alba* and *Avicennia marina* are pioneers in the vegetation succession. These pioneer species, with their complex root network, trap and accrete sediments and cause the land surface to rise relative to the water level over time. This rise creates an environment that inhibits its own existence by promoting recruitment of normal high tide, shade-tolerant species that can withstand salinity greater than 10%, in particular the plants *Rhizophora* spp, *Bruguiera* spp, and *Ceriops* spp. In tidal creeks, species tolerating only low salinity (1-10%) dominate; these include *Sonneratia caseolaris*, *Xylocarpus granatum*, *Heritiera littoralis*, and *Nypa* (Robertson *et al*. 1992). The boundary between the upper limits of mangrove (brackish) and swamp (freshwater) in New Guinea is demarcated by the occurrence of *Sonneratia lanceolata* (Petr 1983). On a long-term scale, the present distribution of mangroves in New Guinea is a result of past episodes of periodic large-scale natural disturbances, including El Nino-mediated, drought-associated fires, lightning strikes (Johns 1993), and geological as well as hydrological disturbances (Semeniuk 1994).

The effect of rising sea level (Pernetta and Osborne 1988) on PNG's mangrove communities suggests that the immediate effect will be drastic changes in the ecological and physiological processes intertwined with the land and marine interface environment occupied by mangrove communities. Species with a specific tolerance within the intertidal zone will migrate landward as their former habitat becomes increasingly marine (Pernetta and Osborne 1988). Such migration will involve disruption and dislodging of established intertidal forest communities and relocation of formerly more terrestrial surfaces as they become inundated by rising sea level, altering ecological and sedimentological processes. Local geomorphological aspects (terrain), the rate of mean sea-level rise, and rate of sediment accretion are major factors that regulate the progradation and regression processes in mangroves (Field 1995). A recent study in the Gulf of Papua suggested an expansion of mangrove forest caused by a sediment accretion rate that exceeded sea level rise (Walsh and Nittrouer 2004).

The loss of PNG’s mangroves has occurred for a number of reasons. For example, the mangrove ecosystem in New Guinea has traditionally been harvested by indigenous people for construction wood, poles, fuel wood, fishing gear, thatched roofs, food, fisheries, and traditional medicine (Spalding *et al.* 1997, Lirbezeit and Rau 2006). These subsistence values are now increasingly being threatened by deforestation for commercial logging, land reclamation, and pollution from large-scale mining tailings (FAO-UNEP 1981, Harris *et al*. 2004, Walsh and Nittrouer 2004). Deforestation from commercial logging and large-scale mining has increased the total sediment load in PNG rivers significantly (1.9 x 10^9 tones yr^{-1}) from a total drainage area of 800,000 km^2, a discharge rate that is equivalent to the total combined loads of rivers draining North America (Milliman 1995). Significant amounts of these sediments end up in the mangrove ecosystem. Mangrove forest loss is approaching disaster proportions near Port Moresby as result of urbanization land reclamation, poaching from urban settlements, and disruptions of natural streams and river courses from road infrastructure development (L. Balun *personal observations*). Mangrove ecosystem in PNG is own by local communities, i.e the people who occupy the land boundaries connecting mangroves stands owned the mangrove. The reduction in mangrove forest may increase unrest among traditional communities, as a result of people who have lost their forest resorting to illegal extraction from neighboring tribes who still have their mangrove forest, which can potential flare up tribal fights. In cases where the entire mangrove communities are lost, coastal tribes may be forced to travel inland to extract their subsistence needs from rain forest, this may again not be easy because every land in PNG is owned by traditional people.

The ecological roles of the mangrove ecosystem as nurseries for fisheries, their involvement in complex marine and terrestrial food chains, biogeochemical cycles, and storm tidal wave and flood retardation, are now recognized in PNG (Robertson *et al.* 1992, 1993, Robertson and Alongi 1995). More recently, the Motupore Research Center (University of Papua New Guinea) and World-Wide Fund for Nature (WWF) pioneered a mangrove rehabilitation and restoration project along the Motuan coasts in Central province (Munkaje *pers. comm*. 2010) near Port Moresby.

Restoring and expansion of degraded mangrove forest is important in combating deforestation pressure on mangrove ecosystem. The rehabilitation of degraded mangrove forests in PNG is currently commissioned under the WWF under United Nation REDD (reduce emission from deforestation and degradation) program primarily to combat carbon emission (Gilman *et al*. 2006). The program can contribute immensely to elevating the subsistence needs of coastal communities. However, the success rates of this REDD mangrove rehabilitation projects are very low (Banka, *pers.comm.*), because their reforestation and afforestation programs presently lack scientific framework (data). Therefore, the results of my studies (Chapter II, III) will contribute positively to improving the establishment rates in mangrove rehabilitation and afforestation in degraded and uninhabited coastal areas respectively.

Before turning to the focus of my research on PNG mangroves, I will first review the broader context of mangrove ecology and physiology to point out important gaps in our understanding of how mangrove systems function. I will argue that occurrence of hyperdiverse mangal system in New Guinea is associated with the underlying ecological processes (vegetation zonation, succession, canopy stratification, and salt excretion ability), which may reflect the prevailing biogeochemical landscape in the intertidal environment. Therefore, the review of these ecological processes is critical in detecting and bridging the knowledge gaps in our understanding of the physiological and functional suites that catalyze coexistence of high species diversity in New Guinea mangroves.

Ecology of mangroves

Mangrove forests display a conspicuous floristic and structural continuum that parallels their underlying biogeochemical environmental gradient (Giesen *et al*. 2007, Hoppe-Speer *et al*. 2011). A review on the ecology of mangrove zonation, structure, succession, and salinity in the subsequent discussion is important in establishing our current knowledge on the ecology of mangrove. This understanding should facilitate the examination of morphological and physiological functional traits associated with the performance of mangrove ecosystem.

Mangrove zonation

Zonation (spatial variation in species' occurrence and abundance with distinct boundaries) in mangrove communities in the intertidal area is striking because of its often monospecific vegetation occurring parallel to the shoreline (Fig.1.5, 1.6) (Davis 1940, Smith 1992, Mendelssohn and McKee 2000). Mangrove zonation typically refers to a discernable pattern in segregation of different species, stature, and productivity of plants across the biogeochemical environmental gradient. This includes variation in the local hydrology, tidal regimes, salinity, geomorphology, nutrient, and temperature (Chapman 1970, Percival and Womerseley 1975, Feller 1995, Boumans *et al*. 2002, Lovelock *et al*. 2004, Milbrandt *et al*. 2006). Zones may be comprised of different architectural forms that represent variations in height and vigor. Several hypotheses have been proposed to explain species' zonation patterns in mangroves: First, zonation reflects land building and plant succession (Davis 1940). This view proposes that mangrove zones represent the different stages of a succession *sere* (gap phase, migration phase, establishment phase, competition phase, and climax phase) as suggested by Clement (1916). Thus, each zone may represent a stage in succession initiated by sediment accretion which is equivalent to gap phase (Watson 1931, Davis 1940). Second, geomorphological processes cause vegetation zonation (Thom 1967). Such a view considers the distribution of vegetation as a function of habitat change where the change is induced by geomorphic processes independent of biotic factors (Thom 1967). It is argued that the processes of sedimentation and subsidence affecting the morphology of large deltas are extremely active. These processes control not only the present shape and composition of landforms but also the dynamic relations between topography and plants. Third, differential dispersal of propagules across a gradient results from a physical "sorting out" of species by tidal action (Rabinowitz 1978). This view argues that species are sorted by tidal activity, which results in deposition of heavier seeds in the deeper areas and lighter species in the shallow areas. Forth, differential predation of propagules across the intertidal zone eliminates some species from certain zones (Smith 1987, Smith *et al*.1989, McKee 1995. This view posits that zonation in mangrove is a function of differential predation between species. Species with highest adult conspecifics are those that experience lowest predation and the reverse for those with low adult density. Fifth, physiological specialization limits distribution of species to certain portions of the gradient where physicochemical conditions differ (Ball 1988, McKee 1993, 1995); and sixth interspecific competition (Ball 1980). This view posits that zonation in mangrove is a result of competition exclusion across an environmental gradient. The perspective taken in my study is that mangrove zonation reflects the interplay between the eustatic or global change (macroclimate and global sea-level changes) and local change (salinity, hydrology, nutrient availability, physiography, geomorphology, tidal duration and lightning damage) (Percival and Womerseley 1975, Medina 1999, Giesen *et al*. 2007).

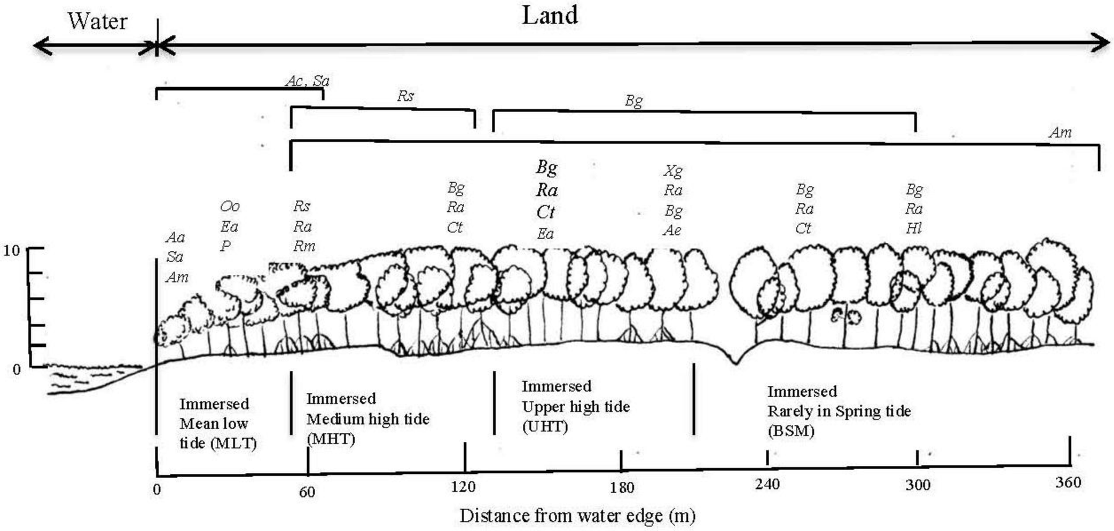

Figure 1.5. A schematic representation of a typical zonation bands in the New Guinea undisturbed mangrove communities. Four recognizable zones are; mean low tide (MLT), medium high tide (MHT), upper high tide (UHT), and back swamp mangrove (BSM). Dominant species within each zones are abbreviated with two letters, a capital letter representing genus and small letter representing species. Where *Aa=Aegialites annulata, Sa-Sonneratia alba, Am=Avicennia marina, Oo-Osbornia octodonta, Ea=Excoecaria agallocha, P=Pemphis* sp*, Rs=Rhizophora stylosa, Ra=Rhizophora apiculata, Rm=Rhizophora mangal, Bg=Bruguiera gymnorrhiza, Ct=Ceriops tagal, Xg=Xylocarpus granatum, Ae=Avicennia eucalyptifolia*, *Hl=Heritiera littoralis*.

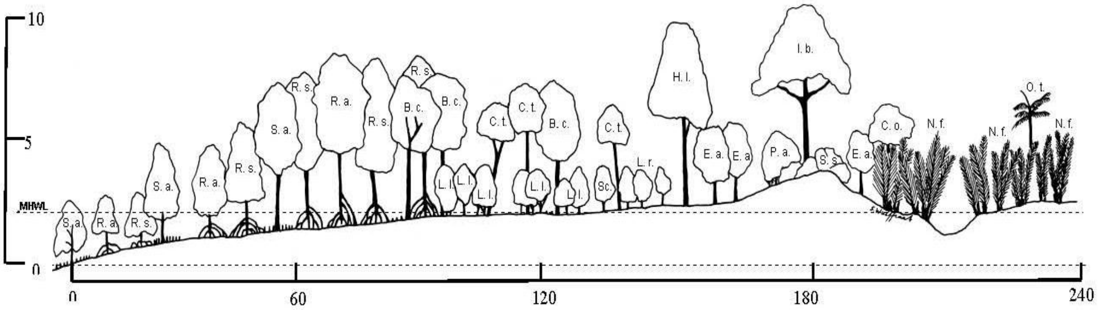

Figure 1.6. Schematic representation of mangrove zonation in Bintan Island, Indonesia. Where *S.a-Sonneratia alba, B.c=Bruguiera cylindrica, S.c-Sonneratia caseolaris, Ea=Excoecaria agallocha, P.a=Pemphis acidula, R.s=Rhizophora stylosa, R.a=Rhizophora apiculata, L.l=Lumnitzera littorea, Ct=Ceriops tagal, I.b=Intsia bijuga, C.o=Cerbera odollum, O.t=Oncosperma tigillarium, Hl=Heritiera littoralis*. *Nypa fruticans,* denoted *N.f.*, forms a monospecific stand in the BSM. This zonation occurs in most of the mangroves in New Guinea.

Forest structure

Besides zonation, forest canopy structure, i.e., spatial distributions of leaf and wood areas, plays a significant role in the interception of photosynthetic photon flux density (PPFD) by leaves, which strongly affects the gas exchange between forests and the atmosphere (Kurachi *et al.* 1993, King and Maindonald 1999, Sterck and Bongers 2001, Law *et al*. 2001, Suwa 2011). It has been estimated that omission of light-penetration aspect of photosynthesis can contribute 10-20% error in photosynthetic estimates (Suwa 2011). Other mangrove attributes, such as species' richness, canopy height, basal area, tree density, age/size class distribution, and understory development, are also influenced by overall forest structure.

Mangrove forests are also classified based on canopy structure. For example, the Florida (USA) mangrove ecosystem has been classified into six forest types, namely; riverine, over-wash, fringe, basin, scrub, and hammock, using canopy structure patterns (Lugo and Snedaker 1974). Species' richness appears to be influenced by temperature, tidal amplitude, rainfall, catchment area, freshwater seepage, and frequency of cyclones (Tomlinson 1986, Lugo and Snedaker 1974).

Another structural characteristic of mangrove forests is the frequent absence of understory species, which are usually found in other forest systems (Janzen 1985). Shrubs, grasses, lianas, and other herbaceous plant species do not usually occur under the closed canopy in mangrove forests. The lack of understory is probably related to the combination of salinity and flooding stresses and low light levels, which exceeds the tolerance limits of plants (Lugo 1986). An understory may develop, for example, where the canopy is open (allowing light penetration to the forest floor) or where rainfall or freshwater runoff lowers salinity levels. There may also be a second layer composed of mangrove seedlings and juveniles, but densities are greatest in light gaps. Forest structure synchronizes with the zonation. With characteristic low stature stands appearing in the MLT zone and increases in the landward direction. The patterns in canopy structure also influence the forest canopy boundary layer, which may have significant influence on the rate of transpiration and photosynthesis. For example, forest canopy gaps often reduce wind speed significantly, resulting in a uniformly low boundary layer (g_b) (*C*. 200-300 mmol m^2 s q) regardless of leaf size. This low boundary layer may result in a stomatal conductance (g_s) typically equal to or greater than g_b conductance. This result then decouples transpiration (*E*) from control by stomata, and subsequently increases g_s (Meinzer *et al*. 1995).

Mangrove succession

In mangal systems, forest gaps result from lightning damage, and not necessarily due to changes in biophysical and chemical gradients (Percival and Wormerseley 1975, Floyd 1977). Nevertheless, the colonization processes are largely dictated by the local salinity and tidal duration, and these variables interact with the ecophysiological performances of species (McKee 1993, Ellison and Farnsworth 1996, Bunt 1996, Matthijs *et al.* 1999). These successional stages can result in the formation of vegetation zones delineated by the disappearance of one or more species and the subsequent appearance of new species that reflect the prevailing biophysical and chemical substrate gradient (Giesen *et al*. 2007). Thus, mangrove succession is a result of competition and exclusion of species with differing tolerances in salinity, anoxic soils, nutrients, and tidal duration (Medina 1999, Giesen *et al*. 2007). In humid tropical regions, salinity decreases in the landward direction such that species with the highest salt tolerance thrive in the seafront, and the least salt tolerant species occur in the back zone. However, in tropical arid areas salinity may increase in the landward direction due to increasing salt deposition further inland. Because of high evaporation in soil surface water, salt deposition subsequently inhibits establishment of tall tree species in the areas having high salt deposition, thus creating salt flats (Medina 1999).

In well-developed mangal systems such as those in PNG and the rest of SEA, four major zones are recognized (Table 1.1, Fig.1.5, 1.6). Zone one is the highly exposed mangrove (HEM) zone, predominantly occupied by species that thrive successfully along the highly exposed seaward side. Species in this zone are inundated during all high tides. This zone is typically dominated by *Avicennia marina, Sonneratia alba, Aegilitis annulata*, *Rhizophora stylosa*, and *R. mucronata*. This zone is referred to as mean low tide (MLT) zone (Fig.1.5).

Zone two is the moderately exposed mangrove (MEM) zone, occupied by mangroves that are less dynamic but also living along exposed seaward sides. The species are inundated during all medium high tides. This zone is typically co-dominated by *Sonneratia alba* and *Avicennia alba*. This zone is also referred to as medium high tide (MHT) zone (Fig.1.5).

Zone three is the central mangrove (CM) zone, which occurs between the seaward and landward bands. This zone is shared by a number of species (*Rhizophora* spp, *Bruguiera* spp and *Xylocarpus* spp) and is considered to be a climax community (Giesen *et al*. 2007).

Zone four is the back mangrove zone (BM), also known as the hind mangrove, rear, or landward mangrove. This zone is situated landward behind the true mangrove belts and is inundated only by spring tides. Species common in this zone include *Excoecaria agallocha, Nypa fruticans, Lumnitzera racemosa, Xylocarpus moluccensis*, and *Pandanus tectora* (Giesen *et al*. 2007). This zone is often grouped with the CM zone and referred to as upper high tide (UHT) zone (Fig.1.5).

Zone five, the brackish stream mangroves (BSM) zone consists of bands of mangroves living along brackish to almost pure fresh water streams that may be occasionally inundated by exceptionally high tides. This zone is predominated by *Sonneratia caseolaris, Cerbera* spp, *Gluta velutina, Xylocarpus granatum*, *Myristica hollrungii,* and *Nypa fruticans* (Fig.1.6).

Salt Excretion

On a local scale, mangrove communities may exhibit floristic and structural gradients that represent gradations in nutrients, salinity, elevation, and exposure to wave action (Giesen *et al*. 2007). Of particular significance, mangroves have evolved an array of morphological and physiological traits to deal with the biophysical and chemical stresses of their hypersaline environment. The requirement to simultaneously balance the salt, water, and energy is a major constraint for mangrove photosynthetic productivity. Water uptake from a salty soil substrate requires energy and special capabilities to exclude ions at the root level, excrete excess salt, or develop a special storage structure that minimizes the risk of damaging the photosynthetic apparatus. These different strategies of dealing with excess salt incur a significant physiological cost (Medina *et al.* 1989, Medina 1999). Energy demand is particularly high for maintaining ion selectivity (high K^+/Na^+ ratios relative to soil water), which depends on the supply of carbohydrates from the leaf canopy as an energy source and the supply of oxygen from the respiratory chain to function efficiently (Sobrado 2004). Most mangroves regulate heavy salt load through the combination of three main mechanisms, namely, salt exclusion, excretion, and accumulation. Species vary in how they combine these three salt regulatory mechanisms (Table 1.2).

The salt exclusion mechanism takes place at the root level, which involves a non-metabolic phenomenon termed ultrafiltration (Scholander 1968). These species exclude salts and extract water from the soil simultaneously.

The excretion of excess salt occurs in the leaves, via specialized salt glands (Fitzgerald *et al.* 1992). The salt-excreting species allow more salt into the xylem than do the non-excretors, but still exclude about 90% of the salts (Scholander *et al.* 1962, Azocar *et al.* 1992). Salt excretion is an active process, as evidenced by ATPase activity in the plasmalemma of the excretory cells (Drennan and Pammenter 1982, Balsamo and Thomson 1995).

The third mangrove salt regulatory mechanism involves accumulating excess salt in vacuoles, transferring excess salt into senescent leaves, or storing excess salt in the bark or the wood (Tomlinson, 1986). Related to this salt accumulation strategy other species synthesize a range of vacuolar solutes (e.g. mannitol, proline, glycine, and asparagine) to help regulate osmotic balance in the face of high salinity (Werner and Stelzer 1990, Popp *et al.* 1993). Although mangroves are immersed in water, it is costly to extract water from a hyper saline environment (Ball *et al*. 1988, Sobrado 2000). Consequently, mangroves must regulate water loss (i.e. transpiration), which occurs during photosynthetic CO_2 uptake. Overall, mangroves have evolved strategies that maintain favorable water balance by regulating the photosynthetic assimilation process and entry of salt in the transpiration stream (i.e. flow of water from root to leaf; Ball 1996, Lovelock and Feller 2003).

Table 1.1: Environmental and floristic zones in the New Guinea mangrove communities. Where: HEM=highly exposed mangrove zone, MEM=medium exposed mangrove zone, CM=central mangrove zone, BM=back zone mangrove, and BSM=brackish stream mangrove zone (adapted from Percival and Womersley 1975).

Pioneers (Shade Tolerant) HEM	Early Secondary (Shade tolerant) MEM	Late Secondary (Shade tolerant) CM	Back-zone (Shade tolerant) BM	Brackish Stream mangrove (Shade tolerant) BSM
Aegialitis annulata	*Rhizophora stylosa*	*Xylocarpus granatum*	*Sonneratia caseolaris*	*Sonneratia caseolaris*
Avicennia marina	*Rhizophora mucronata*	*Xylocarpus rumbhii*	*Nypa fruticans*	*Cynometra ramiflora*
Avicennia alba	*Rhizophora apiculata*	*Xylocarpus australiasicus*	*Dolichandrone spathacea*	*Cerbera floribunda*
Sonneratia alba	*Bruguiera parviflora*	*Bruguiera gymnorhiza*	*Xylocarpus granatum*	*Xylocarpus granatum,*
	Bruguiera cylindrica	*Bruguiera sexangula*	*Avicennia eucalpytifolia*	*Myristica hollrungii*
	Bruguiera exaristata	*Lumnitzera racemosa*	*Aegicerus corniculatum*	*Nypa fruticans*
	Excoecaria agallocha	*Lumnitzera littorea*	*Heritiera littoralis*	*Acrostichum aureum*
	Osbornia octodonta	*Rhizophora lamarckii*	*Acanthus ilicifolius*	*Camptostemon schultzii*

Cont/…

Pioneers (Shade Tolerant) HEM	Early Secondary (Shade tolerant) MEM	Late Secondary (Shade tolerant) CM	Back-zone (Shade tolerant) BM	Brackish Stream mangrove (Shade tolerant) BSM
	Sonneratia ovata	*Avicennia rumphiana*		
	Ceriops tagal	*Avicennia officinalis*		
	Ceriops decandra			

Table 1.2: Mangrove species categorized based on their salt regulatory mechanisms. Superscript, 1, 2, 3, 4, 5, 6 & 7 denotes the solutes involved in salt accumulation: mannitol, proline, glycine betaine, asparagine, stachyose, and purine nucleotide, respectively (Werner and Stelzer 1990, Popp *et al.* 1993)

Salt Regulatory Mechanisms		
Salt exclusion (Ultrafiltration)	Salt excretion	Salt accumulation
Rhizophora spp	*Avicennia* spp	*Lumnitzera* spp^{1}
Bruguiera spp	*Acanthus* spp	*Excoecaria* spp^{1}
Ceriops spp	*Aegiceras* spp	*Aegiceras corniculata*^{2,3}
		Aegialitis annulata^{2,3}
		Laguncularia racemosa^{2,3}
		Avicennia marina^{4,5,6}
		Sonneratia alba$^{6\ 7}$

Salt excretion in mangroves is correlated with substrate salinity and transpiration. For example, excretion in mangrove species exposed to 100% seawater concentration is greater than those exposed to 50% seawater concentration, while the transpiration is higher in species exposed to 50% seawater concentration than those in 100% salt water concentration (Dennan and Pammenter 1982). The total amount of salt excreted is positively correlated with the total amount of water transpired. The rate of salt exudation is also influenced by the diurnal pattern. For example, excretion is minimal during the day and maximal at night (Dennan and Pammenter

1982). The absence of a relationship between xylem sap-salt content and leaf salt content in *Avicennia marina* (Dennan and Pammenter 1982) suggests that salt excretion is not controlled by the process of ion exclusion at the root level. This result also implies that salt arriving at the leaf is sequestrated, potentially in parenchyma tissues and vacuoles (Scholander 1968), before excretion. Kylin and Gee (1970), in their study on *Avicennia nitida,* demonstrated that the Na^+ ion stimulated ATPase from the leaf. Therefore, it can be inferred that the salt balance and secretion in leaves is regulated intrinsically by a light dependent mechanism. Earlier research (Scholander 1968) showed 80% of salt is excluded at the root level through ultrafiltration (a non-metabolic phenomena), with the remaining salt that enters the xylem stream being stored across the xylem, parenchyma tissue, vacuoles, and in the leaf (Scholander 1968, Waisel *et al* 1986).

Mangroves occupy hypersaline, high temperature, and high irradiance environments. Thus, the plants in this habitat must deal simultaneously with these different stresses. Despite growing in an abundant water supply, mangroves transpire slowly to maintain high water use efficiency (Moore *et al*. 1973, Lugo *et al*. 1975, Miller *et al*. 1975, Ball and Farquhar 1984, Ball *et al*. 1988). This low transpiration rate is speculated to be attained by production of high viscosity polymeric substances in the sap, which subsequently limits flow rates and reduces transpiration (Zimmermann *et al.* 1994). The low transpiration rate reduces evaporative cooling of the photosynthetic apparatus. Reduced evaporative cooling can, under high temperature and irradiation, result in a sharp rise in thermal energy in the photosynthetic apparatus (leaf), which may induce photoinhibition and heat damage of the photosynthetic machinery. However, mangroves have evolved morphological and structural mechanisms, which enable them to avoid these damages, namely; leaf inclination and size (reduction of incident radiation) and leaf succulence (buffering of thermal changes) (Medina *et al.* 1989). These adaptive mechanisms also enable mangroves to avoid potential heat damage to their leaves and are regulated by an influx of fresh water from terrestrial runoffs and riverine flow (Medina 1999).

The availability of nutrients, in particular nitrogen (N) and phosphorus (P), in mangrove ecosystems is widely accepted as one of the limiting factors to mangrove productivity. Nutrient poor soil substrates are positively correlated with the sclerophyllous growth habit both in arid regions and in wet areas such as mangrove ecosystems (Feller 1995, 1996, Feller *et al*. 2002, Lovelock *et al.* 2004, 2006). This adaptation strategy to infertile soil comes under the "oligotrophic-xeromorphism hypothesis" (Givnish 1979, Sobrado and Medina 1980), which states that xeromorphism in wet environments, including the mangrove ecosystem, is a manifestation of low soil phosphate availability. The sclerophyllous leaves of mangroves have physical and chemical properties that reduce decomposition rates, therefore, slowing nutrient turnover. Xeromorphism in mangroves induces a longer leaf life span, which in turn promotes a high biomass nutrient retention rate. The overall emerging view of xeromorphism is that it is an adaptation for nutrient conservation in nutrient-poor habitats (Small 1972, Janzen 1974, Chapin 1980, Chabot and Hicks 1982, Horner *et al.* 1988).

Despite attracting considerable interest from botanists and ecosystem scientists over the last 60 years, data on mangrove productivity are limited. Interestingly, recent attempts to better understand mangrove productivity in low diversity mangal systems (i.e., southern Florida, USA) suggested that mangrove ecosystems have higher primary productivity than some tropical lowland rainforests (TRF; Mitsch and Gosselink 2000) as well as more dynamic biogeochemical cycles (*et al.* 2008b). Because primary productivity is positively correlated with species' diversity, it could be argued that mangroves with relatively high primary productivity should have higher diversity than equivalent TRF habitats. However, the reverse is true; mangrove diversity is much lower than that of lowland rainforests (Gentry 1982). What explains this possible inverse association between productivity and diversity in mangrove forests? A key problem is that it lacks the requisite physiological data on mangroves in their natural forests to tell whether or not mangroves are capable of high versus of low photosynthetic potential - the basis for primary productivity.

A long standing hypothesis is that the physiological stresses experienced in the coastal interface enforce low photosynthetic productivity of mangrove species. Mangroves are overly immersed in high-salinity water and exposed to a high irradiance environment experiencing physiological drought. Consistent with a hypothesis of low photosynthetic capacity, most (but not all!) mangrove forests are relatively short compared to adjacent non-coastal tropical forest vegetation (Paijmans *et al*. 1976, Whitmore 1996). Accordingly, it is essential that mangroves maintain a balance between salt loads in the transpiration stream and photosynthetic carbon assimilation because salt inhibits photosynthetic biochemistry (Popp 1984, Naidoo 1987). As discussed elsewhere in this chapter, mangroves have evolved salt regulatory mechanisms to avoid access salt in the photosynthetic sites (leaves). Mangrove leaves accordingly must deal simultaneously with gas exchange and salt excretion. A number of studies have shown that photosynthetic carbon assimilation and growth rate declined with increasing substrate salinity concentration (Clough *et al*. 1982, Ball and Farquhar 1984, Clough 1984, Sobrado 1999). Transpiration rate (E) has also been shown to decline with increasing salinity gradient (Drennan and Pammenter 1982). Increased substrate salinity coupled with drought has also been reported to reduce A_{max} (Azocar *et al*. 1992, Naidoo and von Willert 1994, Smith *et al*. 1989). Photosynthetic carbon assimilation rates are positively correlated with leaf nitrogen content (Suwa *et al.* 2006).

Most studies on gas exchange capacity in mangrove support the long standing paradigm that mangroves are very conservative and subsequently have high water use efficiency, therefore low photosynthetic carbon assimilation rates (A_{max}) typically less than 8 µmol CO_2 m^{-2} s^{-1} (Ball and Farquhar check spelling1984, Clough *et al*. 1984, Brugnoli and Björkman 1992, Smith *et al.* 1992, Passioura *et al*. 1992, Naidoo and von Willert 1994, Sobrado 1999). Typical maximal photosynthetic carbon assimilation capacities in angiosperms are ~10 µmol CO_2 $m^{-2}s^{-1}$ (Brodribb *et al*. 2007, Brodribb and Feild 2010). Therefore any A_{max} below 10 µmol CO_2 $m^{-2}s^{-1}$ can be considered to be low. A_{max} of mangroves also varies markedly with season. For example, a study on *Rhizophora mangle* and *Laguncularia racemosa* in a glasshouse experiment on the effects of different hydroperiods produced mean A_{max} of 8.1 ± 0.9 µmol CO_2 m^{-2} s^{-1} and 9.7±0.7 µmol CO_2 m^{-2} s^{-1} respectively. In dry season, the A_{max} was reduced from 9.6 ± 2.0 to 4.7 ± 2.5 between plants low and high salinity sites, respectively (Kraus *et al.* 2006). Glasshouse studies on a limited number of mangrove taxa have also generally reported A_{max} values less than 10 µmol CO_2 m^{-2} s^{-1} (Ball and Farquhar 1984; Sobrado and Ball 1999, Sobrado 2005). Most of the above studies focused on single species and under glasshouse environments and their general application for understanding ecological and physiological processes in diverse mangrove ecosystems in the field are limited.

Interestingly, there a few field studies that found mangrove trees attained high A_{max} and transpiration (*E*) rates. For example, a study from PNG and tropical Australia mangroves reported a A_{max} of 22 µmol CO_2 $m^{-2}s^{-1}$ in *Avicennia germinans* (Clough and Sim 1989). Another study from Australia focused on *Rhizophora apiculata* reported an A_{max} of 25 µmol CO_2 $m^{-2}s^{-1}$ (Clough, 1992). Also, *Rhizophora mangle* from Florida reportedly possessed an A_{max} at 18 µmol CO_2 $m^{-2}s^{-1}$ (Barr *et al*. 2009). Finally, *Rhizophora stylosa* from measured an A_{max} of 17 µmol

CO_2 $m^{-2}s^{-1}$ (Suwa and Hagihara 2006). The average photosynthetic carbon assimilation rate in angiosperms is ~ 8 µmol CO_2 $m^{-2}s^{-1}$ (Brodribb *et al*. 2007, Brodribb and Feild 2010). These high A_{max} values for mangroves are similar to some of the fastest growing tropical lowland rainforest trees including pioneers (Mooney *et al*. 1978, Bazzaz and Pickett 1980, Larcher 1995, Brodribb *et al*. 2007, Brodribb and Feild 2010, Feild *et al*. 2011b). These limited studies suggest a possibility that mangroves can attain high photosynthetic gas exchange capacity. However, as to whether the same is true for the rest of the mangrove species remains unclear without considering the performance of high diversity mangrove communities. In addition, none of these previous studies have looked at the hydraulic side of the photosynthetic equation for mangroves. Therefore, my study will for the first time examine the photosynthetic gas exchange capacity, including water use, for the broadest spectrum of mangrove taxa so far sampled from six mangrove communities in PNG.

Dissertation Focus: Understanding ecophysiological diversity in hyperdiverse mangrove communities in PNG

Nearly all previous studies on mangrove ecophysiology have focused on mangrove communities of low diversity or these studies examined comparative mangrove responses under artificial glasshouse studies (Sperry and Tyree 1988, Drennan and Pammenter 1982, Ball 1988, Ball and Farquhar 1988, Ball and Pidsley 1995, Youseff and Saenger 1998, Sobrado and Ball 1999, 2002, 2006, Cheeseman and Lovelock 2004, Ewers *et al*. 2004, Lovelock *et al*. 2004, 2006, Lopez-Portillo *et al*. 2005, Schmitz *et al*. 2006). This focus is understandable given that mangrove forests are harsh to work in for researchers (hot, humid, malaria) and their physiological equipment and many of the most diverse and intact mangrove forests now only occur in very remote tropical areas. Thus, our current knowledge of the ecological and functional role of global mangrove ecosystems remains limited to situations that do not approximate very diverse mangrove ecosystems. Functional diversity in plants has a prime influence on ecosystem processes, and, subsequently, ecosystem services (Díaz and Cabido 2001, Vendramini *et al.* 2001). Functional diversity also influences specific ecosystem characteristics, including nutrient cycling, hydrology, microclimate, disturbance, species' interactions (Eviner and Chapin 2003), invisibility-openness to invasion (Daehler 2003), stability (Díaz and Cabido 2001), productivity, and resource-use strategies (Vendramin *et al.* 2001).

For many plant physiological traits, photosynthesis and transpiration can be directly linked to functions that influence ecosystem processes. These traits are often correlated with other leaf-level traits, both morphological and physiological (Wright *et al*. 2005a), giving rise to trait associations commonly referred to as "functional suites". For example, leaf traits such as leaf mass per unit area (LMA), foliar nitrogen (N), leaf life span (LLS) (Chapin 1993, Reich *et al*. 1997, Sanquist and Cordell 2007, Santiago and Wright 2007), and leaf vein density (Brodribb *et al*. 2007, Boyce *et al*. 2009, Brodribb 2009, Brodribb and Feild 2010) have been shown to co-vary with photosynthesis. Furthermore, many such trait pairs have a common scaling relationship across broad habitats, climates, and phylogenetic levels (Reich *et al*. 1997, Wright *et al*. 2005b). Measurements of the diversity of such functional suites and scaling relationships within hyper-diverse mangrove communities in New Guinea are central to a better understanding of the adaptive value of these suites and their influences on mangrove ecosystems and the interconnected terrestrial and marine ecosystems. Measuring anatomical features related to photosynthetic-hydraulic performances of mangroves has the added attraction that they are easier to measure than physiological methods and can be applied to much larger number of taxa. Also anatomical traits of plant performance may offer more time-integrated signatures of plant performance as compared to physiological measurements that are made on a limited number days. My dissertation will therefore focus on measuring functional suites from six hyperdiverse mangrove communities in Papua New Guinea. I will also relate these measures to physiological measures for the first time to test how reliable structural traits yield insights into mangrove plant function.

Studies based on high diversity mangrove communities are also critical to a better understanding of the ecological and functional role of global mangrove ecosystems. High diversity mangrove communities are comprised of a wide range of unrelated plant species, which show strong morphological and functional convergence (Tomlinson, 1986). These convergences seemingly represent a biological strategy related to the unique, physiologically challenging demands of being a plant at the land-ocean interface. Thus, research on the ecophysiological characteristics of highly diverse mangrove ecosystems can contribute to a sound understanding of global mangrove ecosystems. New Guinea is the center of mangrove diversity in the world and therefore has potentially important key communities for shedding new insights into the global ecological and functional role of mangroves. However, there is very little research done on the functional ecology of these diverse mangrove communities in New Guinea. Until hyperdiverse mangal communities, such as those in New Guinea (which have up to 30 species in a single mangal catchment) are studied, broad generalizations about mangrove productivity and function are impossible. It is the goal of my dissertation to investigate the diversity of leaf and wood function in hyper-diverse New Guinea mangrove communities as a model system for better understanding how the mangrove ecosystem, in general, functions.

I will test the hypothesis that mangroves exhibit a narrow range of functional performances despite their wide-ranging phylogenetic origins. The results of my work will fill the existing knowledge gap in our understanding of functional traits controlling the distribution of New Guinea's hyperdiverse mangrove forests. The results will provide data on the ecological and functional characteristics of mangrove species, which will contribute to designing appropriate management strategies for rehabilitation of degraded mangrove ecosystems.

My dissertation research focuses on two research areas. In Chapter two, I will discuss the relationship of leaf ecomorphology and mangrove functional ecology. The leaf ecomorphic traits I will report for the first time for mangroves include: vein density ($D_{V,}$ mm mm^{-2}), leaf mass per area (LMA, g cm^{-2}) and the relation between these measures with net maximum photosynthetic assimilation rate (A_{max}, µmol CO_2 $m^{-2}s^{-1}$) and stomatal gas exchange (g_s, mmol H_2O $m^{-2}s^{-1}$). Understanding these variables is critically important to clarifying the productivity relations and the hydraulic costs for productivity of the New Guinea mangrove ecosystems.

I then will examine relations of ecomorphic traits to functional traits to understand for the first time how the New Guinea species are performing to attain such a high diversity level of coexistence in a narrow ecological space. The LMA trait is used as a proxy for resource-use strategy and relative growth rate (linked to nutrient availability) in the New Guinea mangroves. I also further explore the relationships between leaf functional traits with mangrove plant growth form as well as zonation.

In Chapter three, I will examine how functional traits of mangrove woods are related to leaf performance. The focus on wood is key because wood: (1) reflects a long term investment in resources by plants and thus wood traits may offer more accurate assessments of mangrove photosynthetic-hydraulic function (Poorter *et al*. 2009); and (2) wood represents a key storage pool of carbon and understanding how mangrove wood function is critical for obtaining estimates of above ground carbon storage for mangrove ecosystems. Thus, I propose to examine how wood density (P_{wood}, g cm^{-3}) is related to structural traits related to wood hydraulic performance (vessel density, number of vessels mm-2 and vessel diameter, mm), as well as functional or hydraulic conductance traits of mangrove stems. The purpose of Chapter three is to understand how and what mangrove wood is doing in response to the hydraulic demands of the whole plant which are attributed to the acclaimed high primary productivity. I will also explore the relationships how wood functional trait variation is related to mangrove zonation and growth form. Again, these data will provide another set of comparisons to test my overall hypothesis that mangroves exhibit narrow functional performance despite their diverse origins.

Finally, I conclude in Chapter four that summarizes the relative contributions of leaf and wood functional traits as they operate in a hyperdiverse mangrove community. I discuss the emergent implications for my research in understanding mangrove plant function in relation to coastal ecosystem function and mangrove ecosystem restoration. I will also offer a new plant-trait informed discussion of potentially fruitful future research directions on the functional ecology of mangrove ecosystems.

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APPENDICES

Appendix 1. World distribution of mangrove by country and their respective area size in hectares adapted from (FAO, 2007) Denotation superscript (*) indicates Shearman (2010) as source.

Country	**Area (000's Ha)**	**Country**	**Area (000's Ha)**
Angola	125	Jamaica	7
Australia	1150	Kampuchea	10
Bangladesh	450	Kenya	45
Belize	75	Liberia	20
Brasil	2500	Madagascar	300
Brunei	7	Malaysia	674
Burma	812	Mexico	660
Cameroon	272	Mozambique	455
Colombia	440	Nicaragua	60
Costa Rica	39	Nigeria	970
Cuba	400	Pakistan	345

Dominican Republic	9	Panama	486
Ecuador	235	Papua New Guinea	592*
Country	**Area (000's Ha)**	**Country**	**Area (000's Ha)**
El Salvador	45	Peru	28
Equatorial Guinea	20	Philippines	240
Fiji	39	Senegal	169
Gabon	140	Sierra Leone	170
Gambia	60	Somalia	20
Guatemala	50	Sri Lanka	4
Guinea	260	Surinam	115
Guinea-Bissau	230	Tanzania	96
Guyana Frances	55	Thailand	287
Guyana	150	Trinidad & Tobago	4
Haiti	18	Venezuela	260
Honduras	145	Vietnam	320
India	96	Zaire	50
Indonesia	2500		

CHAPTER II: DIVERSITY OF LEAF PRODUCTIVITY FUNCTIONA FROM HYPERDIVERSE NEW GUINEA MANGROVE ECOSYSTEM

ABSTRACT

Despite being immersed in water, mangroves experience a physiological drought (low water potentials) at the leaf level due to the high salinity of the water. Because of being exposed to chronic drought, mangroves are viewed as highly conservative plants, functioning with high water use efficiency and low photosynthetic assimilation rates. Together, these features are thought to constrain mangroves to a narrow range of functional performances. However, the ecophysiological diversity of mangrove forest trees remains ill-defined. The present study tests the hypothesis that mangroves exhibit a narrow leaf productivity functional performance by examining variation in plant functional traits and physiological performances of mangrove plants representing a wide range of phylogenetic affinities from Papua New Guinea.

Investigation of photosynthetic gas exchange capacity of 31 co-existing mangrove species in six hyperdiverse mangrove communities in New Guinea revealed that different zonation bands in mangrove forests showed significant differences in photosynthetic carbon assimilation rate (A_{max}; $F_{2,12} = 3.89$, $P < 0.05$) and maximum stomatal conductance rate (g_{smax}; $F_{2,10} = 4.69$, $P < 0.04$). Maximum A_{max} (19.20 ± 0.88 µmol CO_2 $m^{-2}s^{-1}$) and g_{smax} (0.24 ± 0.03 mmol $m^{-2}s^{-1}$) were reported in mean low tide (MLT) zone that is the most exposed to the salt water.

Photosynthetic gas exchange capacity among the three growth forms (shrub, small-medium tree, and large tree) differed significantly (A_{max}; $F_{2,15} = 4.20$, $P < 0.04$; g_{smax}; $F_{2,9} = 5.75$, $P < 0.03$).

Vein density (D_V) differed significantly among the zones ($F_{2,17} = 3.83$, < 0.04) and growth forms ($F_{2,18} = 7.55$, $P < 0.004$). Highest D_V was measured in *Avicennia marina*

(15.24±0.42 mm mm^{-2}) and the lowest was measured in *Acanthus ilicifolius* (4.84±0.23 mm mm^{-2}). D_V correlated positively to the photosynthetic traits A_{max} ($R^2 = 0.68$, $P < 0.001$) and g_{smax} ($R^2 = 0.68$, $P < 0.001$).

The resource-use strategy trait, leaf mass per area (LMA, g m^{-2}), which is a good predictor of growth rate differed significantly among zones ($F_{2,10} = 9.89$, $P < 0.004$) but not growth forms. Highest LMA (209.52±7.89 g m^{-2}) was observed in the mean low tide (MLT) zone and decreased in landward direction. The highest LMA was observed in shrub growth form, followed by small-medium trees and large trees, respectively. LMA differed significantly among different salt excretion modes ($F_{2,20} = 8.81$, $P < 0.002$).

The significant differences in means of A_{max}, g_{smax}, D_V, and LMA among zones and growth forms in mangal systems indicate that mangroves are highly partitioned in their ecophysiological niche across biogeochemical environmental gradients. An important implication on mangrove restoration is that mangroves are not just a "plug and play" plant assemblage that can be used randomly to revegetate degraded coastlines. Thus, a comprehensive understanding of the functional traits of mangrove species is critical for any successful vegetation restoration efforts.

INTRODUCTION

Mangroves comprise shrubs and tree species of widely unrelated taxa, which occupy usually calm inter-tidal zones along coastal shorelines and river deltas of the tropical and subtropical latitudes (Lear and Turner 1977, Belperio 1979). These phylogenetically distant taxa exhibit convergences in their overall functional and morphological characteristics (Lugo and Snedekar 1974, Tomlinson 1986). For example, mangroves have evolved similar functional, ecological, and morphological characters, such as aerial roots, thick succulent leaves, glossy color, leaf position > 90^o angled, and viviparous reproduction (Tomlinson 1986). Mangrove communities often exhibit spatial zonation reflecting the gradation in the physical and biogeochemical environment with species' specialization (MacNae 1968, Percival and Womerseley 1975, Feller 1995, Boumans *et al*. 2002, Lovelock *et al*. 2004, Milbrandt *et al*. 2006). The structural and functional convergence among mangrove species contribute to successful development of a community in a hyper-saline environment form the core of much of the early ecophysiological research on mangroves (Scholander *et al*. 1966, MacNae 1968, Lugo and Snedekar 1974, Ball and Farquhar 1984, Flowers *et al.* 1986, Naidoo 1987, 1990, Ball 1988, Ball *et al.* 1988). There is a consensus that the structural and floristic spatial distribution of the mangal system parallels the different spatial zones in which they grow. These spatial zones reflect gradations in biogeochemical factors (tides, nutrients, rainfall, temperature, and stressors like hurricanes, drought, and salt accumulation; Ball and Farquhar 1984, Ball *et al.* 1987, Ball *et al*. 1988, Bunt 1996, Matthijs *et al*. 1999, Sobrado and Ball 1999, Sobrado 2001, Sobrado 2004, Hoppe-Speer *et al*. 2011, Rivera-Monroy *et al*. 2004). Because the action of these factors varies widely over geographic regions, mangrove stands exhibit wide regional and local variation in structural characteristics. In high diversity mangrove communities, structural variation is even greater (English *et al.* 1997).

Most studies on mangrove communities have been concerned with understanding their biology, composition, distribution, and abundance (Ellison and Stoddart 1991, Alongi 2002, Alongi *et al*. 2004, Duke *et al.* 2007, Alongi 2008, Gilman *et al*. 2008, Polidoro *et al*. 2010). Functional studies on mangrove communities, which search for understanding of how mangroves balance and maintain primary productivity and biogeochemical processes, are increasingly gaining interest (Ball and Farquhar 1984, Flowers *et al.* 1986, Naidoo 1987, Ball 1988, Ball *et al.* 1988, Sobrado 1999, Schmitz *et al*. 2006, Donato *et al*. 2011). Most of these studies focus on a single species (Sobrado 1999, Khan *et al*. 2004, Sobrado 2005, Schmitz *et al*. 2006, Suwa and Hagihara 2006, Suwa 211) while others involve contrasting a few species (Andrews *et al*. 1984, Ball and Farquhar 1984a, 1984b, Andrew and Muller 1985), examining low diversity mangrove communities or conducting glass house experiments (Ball and Farquhar 1984a, 1984b, Krauss *et al*. 2006). Comparative primary productivity data from field based studies of high diversity mangrove communities are lacking.

Data on photosynthetic carbon assimilation (a major determinant of productivity in plants) from high diversity mangrove communities are lacking. This gap in the mangrove primary productivity data is the motivation for my study. I examined the mangrove productivity and mechanisms responsible for the observed patterns in six, hyperdiverse mangrove communities in PNG. Specially, I focussed on the primary driver of primary productivity – leaf photosynthesis. I examined leaf and photosynthetic functional traits, defined as “any attribute that has potentially significant influence on establishment, survival and fitness” (Reich *et al*. 2003) to shed light on the primary productivity relations of mangroves.

Why the focus on leaves? Leaves play a significant role in photosynthesis in contrast to stem photosynthesis. For example, leaves have an A_{max} (maximum light carbon assimilation rate) of 20 µmol CO_2 $m^{-2}s^{-1}$ in temperate species (Witmann *et al*. 2001) and ~13 to 25 µmol CO_2 $m^{-2}s^{-1}$ in tropical species (Brodribb and Feild 2010) and stem photosynthesis is ~0.72 to 3.73 µmol CO_2 $m^{-2}s^{-1}$ in temperate species (Berveiller *et al*. 2006). Leaves fundamentally influence photosynthesis and transpiration. In turn, these processes have a cascading influence on biogeochemical and hydrological processes in terrestrial ecosystems (Field *et al* 1998, Boyce *et al.* 2002, Boyce 2005, Beer *et al*. 2010, Brodribb and Feild 2010, Feild *et al*. 2011a, b). High primary productivity is directly related to the photosynthetic capacity of plants (Reich *et al*. 1977, Brodribb *et al*. 2007, Boyce *et al.* 2009, Brodribb and Feild 2010, Feild *et al*. 2011a, b). Primary productivity, forest stature, and growth rates in mangrove forests are directly correlated to photosynthetic functional traits of species (A_{max}, µmol CO_2 m^{-2} s^{-1}; g_{smax}, mmol H_2O m^{-2} s^{-1}), which are mechanistically linked to the hydraulic capacity of a species (Brodribb *et al*. 2007, Boyce *et al.* 2009, Brodribb and Feild 2010). The photosynthetic capacity of plants is also constrained by water use efficiency (WUE) of a species in response to an array of environmental stresses a species is subjected to over its life history (Ball *et al.* 1988, Fonti *et al*. 2010). For example, mangroves despite being abundantly immersed in water have been reported to function with high WUE because of the high cost in extracting water from a highly saline substrate (Ball 1988, Sobrado 2000, 2004). Mangroves, which are subjected to constant hypersaline conditions, are structured to deal simultaneously with balancing high ionic concentration in the transpiration stream, excess salt, water loss, and photosynthetic assimilation functions. At the same time, they must protect the cytoplasm from damage otherwise incurred if cellular functions are exposed to seawater (Ball and Farquhar 1984, Flowers *et al.* 1986, Naidoo 1987, Ball 1996, Fonti *et al*.

2010). Protection from cytoplasm damage due to excessive salts is attained through salt exclusion at the root level by ultrafiltration (Scholander *et al.* 1966, 1968), salt accumulation in storage tissues (Popp 1984), and salt secretion in leaves via leaf glands (Atkinson *et al*. 1967, Ball 1988, Fitzgerald *et al*. 1992). Salt secreting species *Avicennia marina* secretes salt from alternating leaf sides (adaxial or abaxial) in different sites (Carpenter *et al.* 1990). Although there has been long recognition of the importance of these processes, there remains a limited understanding of how leaves of different mangrove species function in the field.

In recent years, a large body of evidence has emerged about how to describe the resource-use physiology, especially leaf traits associated with CO_2-H_20 strategies of nearly any plant leaf. For example, leaf traits (vein density, D_V; leaf mass area, LMA) have strong influence on photosynthetic gas exchange capacity of a plant and nitrogen use efficiency respectively, and subsequently productivity (Brodribb *et al*. 2007, Boyce *et al*. 2009, Brodribb and Feild 2010, Feild *et al*. 2011a). These traits largely quantify how well a species gains carbon through photosynthesis in relation to the loss of water out of the leaf to "eat" the air during photosynthesis. First of these traits is leaf mass per area (LMA, g m^{-2}) — defined as previously photosynthesized dry mass per unit of light-intercepting area. LMA is a trait strongly correlated to a plant’s resource-use strategy and growth rate (Grime *et al*. 1997, Wilson *et al*. 1999, Beer *et al*. 2010). For example, low LMA is linked to a resource-poor habitat (sclerophyllous and succulent plants) in which differential allocation for storage and defense as well as long lifespan is favored. On the other hand, high LMA is associated with resource-rich habitat with preferential allocation to photosynthesis and growth (Cunningham *et al*. 1999, Vendramini *et al*. 2001). The xeromorphic (sclerophyllous) traits (thick lamina, high LMA, long leaf life span) exhibited by mangroves (Table 2.0) are hypothesized as a nutrient conservation strategy for a low nutrient environment (Givnish 1979, Sobrado and Medina 1980, Medina *et al*. 1989). Therefore, measurement of LMA allows insights into many aspects of plant functions, such as gas exchange (Field and Mooney 1986, Poorter and Bongers 2006), hydraulic and photosynthetic proficiency (Reich *et al.* 1997, Poorter and Bongers 2006, Brodribb *et al*. 2007), decomposition rate (Cornelissen and Thompson 1997, Cornelissen *et al*. 1999), leaf toughness/succulence (Choong *et al*. 1992), relative growth rate (Ball 1988), and leaf life span (Wright *et al*. 2005a, Wright *et al*. 2005b). LMA has also served as an indicator of salinity and nutrient gradient (Ball 1988, Wright *et al*. 2005a) and the resource-use strategy of plants, which relate to photosynthetic carbon assimilation rate, productivity, and growth rate (Williams *et al*. 1987, 1989). The LMA trait in mangroves therefore can provide reliable inferences regarding multiple leaf functional aspects of mangroves. In the present study, I use the LMA trait coupled with leaf vein density (see below) and photosynthetic gas exchange traits (A_{max}, g_{smax}) to understand the productivity and functional performance of mangroves making up a hyperdiverse mangrove ecosystem.

Table 2.0: The 27 mangrove species which exhibit xeromorphic traits (thick leaf). The 27 species are categorized as xeromorphics based on their leaf structure (tough, leathery leaves with moderate to high degree of sclerification) (Schulze 1982, Vendramini *et al*. 2001).

Family	**Scientific Names (Species)**	**Xeromorphic Traits**
Acanthaceae	*Acanthus ilicifolius*	Thick leaf
Acanthaceae	*Avicennia alba*	Thick leaf
Acanthaceae	*Avicennia eucalyptifolia*	Thick leaf
Acanthaceae	*Avicennia marina*	Thick leaf
Acanthaceae	*Avicennia officinalis*	Thick leaf
Combretaceae	*Luminitzera racemosa*	Thick leaf
Euphorbiaceae	*Excoecaria agallocha*	Thick leaf
Icacinaceae	*Stemonurus apicalis*	Thick leaf
Meliaceae	*Xylocarpus australasicus*	Thick leaf
Meliaceae	*Xylocarpus granatum*	Thick leaf
Meliaceae	*Xylocarpus rumphii*	Thick leaf
Myrsinaceae	*Aegiceras corniculatum*	Thick leaf
Myrtaceae	*Osbornia octodonta*	Thick leaf
Plumbaginaceae	*Aegilitis annulata*	Thick leaf
Rhizophoraceae	*Bruguiera cylindrica*	Thick leaf
Rhizophoraceae	*Bruguiera exaristata*	Thick leaf
Rhizophoraceae	*Bruguiera gymnorrhiza*	Thick leaf
Rhizophoraceae	*Bruguiera parviflora*	Thick leaf

Family	**Scientific Names (Species)**	**Xeromorphic Traits**
Rhizophoraceae	*Bruguiera sexangula*	Thick leaf
Rhizophoraceae	*Ceriops decandra*	Thick leaf
Rhizophoraceae	*Ceriops tagal*	Thick leaf
Rhizophoraceae	*Rhizophora apiculata*	Thick leaf
Rhizophoraceae	*Rhizophora mucronata*	Thick leaf
Rhizophoraceae	*Rhizophora stylosa*	Thick leaf
Rubiaceae	*Scyphiphora hydrophyllacea*	Thick leaf
Sonneratiaceae	*Sonneratia alba*	Thick leaf
Sterculiaceae	*Heritiera littoralis*	Thick leaf

Another important leaf functional trait reflecting the tradeoff of water for carbon is vein density (D_V). D_V has been found to closely correlate to the following photosynthetic functional traits: A_{max} –the light-saturated net photosynthetic carbon assimilation rate and g_{smax}-the maximum stomatal conductance rate (Brodribb *et al*. 2007, Boyce *et al*. 2009, Brodribb and Feild 2010, Feild *et al*. 2011a, b). For example, evolution of leaf structural diversity involving shift in low vein density leaf ~1 mm mm^{-2} to ~8 mm mm^{-2} (mean of the total length of vein branches per mm^{-2} of leaf tissue) in the last 400 million years is a key innovation to dramatic increases in photosynthetic capacity of terrestrial plant diversity (Brodribb and Feild 2010). Indeed, D_V evolution has been viewed as the mechanism for the unprecedented leap in floristic diversification during the Cretaceous (Feild *et al*. 2011b). The intimate link between D_V, A_{max}, and g_{smax} validates their use in defining how plant leaves function (Brodribb *et al.* 2007). The relation between D_V and A_{max} is clearly mechanistic since vein branching or vein density - determines the water supply capacity for CO_2 uptake (Brodribb *et al*. 2007).

Photosynthetic gas exchange studies of mangrove ecosystems (Ball and Farquhar (1984), Ball 1988, Ball *et al*. 1988, Sobrado 2000) indicate that net carbon assimilation and productivity in mangroves are generally lower than that of the tropical rain forest ecosystem (~10μmol CO_2 m^{-2}s^{-1}; Larcher 1995, Brodribb *et al*. 2007). However, a recent study on carbon content in mangrove ecosystems revealed these ecosystems have the most carbon-rich forests in the tropics, containing on average 1.023 x 10^{6} kg carbon per hectare, of which 49-98% is stored in the soil (Donato *et al*. 2011). Mangrove ecosystem is undoubtedly the most productive vegetation biome in the world. Notably, it sequestrates ~7 to 11-fold greater carbon in the above ground biomass than tropical rain forest (9.0 x 10^{4} kg C ha^{-1}yr^{-1} in Southeast Asia tropical rain forest (Iverson *et al*. 1993) and 1.5 x 10^{4} kg C ha^{-1}yr^{-1} in Amazon rain forest (Mahli and Grace 2000). Contrasting views of mangrove photosynthetic gas exchange capacity and productivity highlight the disparity in research findings regarding the functional ecology of mangrove ecosystems. Consequently, it is difficult to make comparisons on the net carbon assimilation, productivity, and growth rates for the global mangrove ecosystem. Lack of comparative studies from high diversity mangrove communities limits our ability to make comparisons on carbon assimilation and biomass productivity for global area of mangrove with other forest communities. My study on the high diversity mangrove communities in New Guinea aimed at closing this knowledge gap.

My a priori hypothesis is that mangrove species exhibit narrow functional performance despite their wide phylogenetic affinities. My hypothesis emerges from the long held view that mangroves are highly conservative with high water use efficiency, low photosynthetic rate, and low primary productivity (Ball and Farquhar 1984, Ball 1988, Ball *et al*. 1988, Sobrado and Ball 1999, Naidoo and Chirkoot 2004, Naidoo 2006). To test my hypothesis, I examined the patterns in leaf functional traits (D_V, LMA, A_{max}, and g_{smax}) across biogeochemical environmental gradient (zonation, different zones demarcated by different tide levels, and species composition) and different growth forms in light of mangrove productivity and growth rates. Specifically, I had the following objectives: (a) determine if differences exist in leaf vein density (D_V), leaf mass per area (LMA), and photosynthetic gas exchange capacity (A_{max}, g_{smax}). I will measure D_V from mean of total vein branch length per mm^{-2}. I will measure LMA (g cm^{-2}) from the mean of dry mass per leaf area among taxa, zones, and growth forms, (b) investigate the relationships between leaf functional traits, productivity, and growth, (c) determine the constraints imposed by these leaf functional traits on mangrove photosynthetic carbon assimilation, stomatal gas exchange, and their subsequent influence on productivity, growth, and survival, and (d) finally, link how these leaf functional traits scale up (related or linked) to hydraulic functional traits from my second study (Chapter Three).

MATERIALS AND METHODS

Field Site and Plant species

Location and Climate

Research was conducted in six tropical mangrove communities in Papua New Guinea (PNG), namely; the Motupore Island mangrove (09°31’S, 147°17’5 E); Bootless Bay mangrove (09°30’S, 147°16’E) within Central province; Labu mangrove (06°45’S146°57’E); Wangang mangrove (06°44’S, 147°01’E) within Morobe province; Riwo mangrove (05°08’S, 145°47’E); and Madang airport mangrove (05°12’S, 145°47) within Madang province (Fig.2.0).

Motupore Island is situated in Bootless Bay ~15km SE of Port Moresby, the capital of PNG. The island is ~18 ha (45 acres), mostly hilly, and about 200 m offshore of Bootless mainland. The Motupore Island and Bootless study sites experience similar climatic conditions (Table 2.1, McAlpine *et al*. 1983). The two areas experience a prolonged dry period from June to October. Both sites receive about 1 to 2 rain days a month during this prolonged dry period.

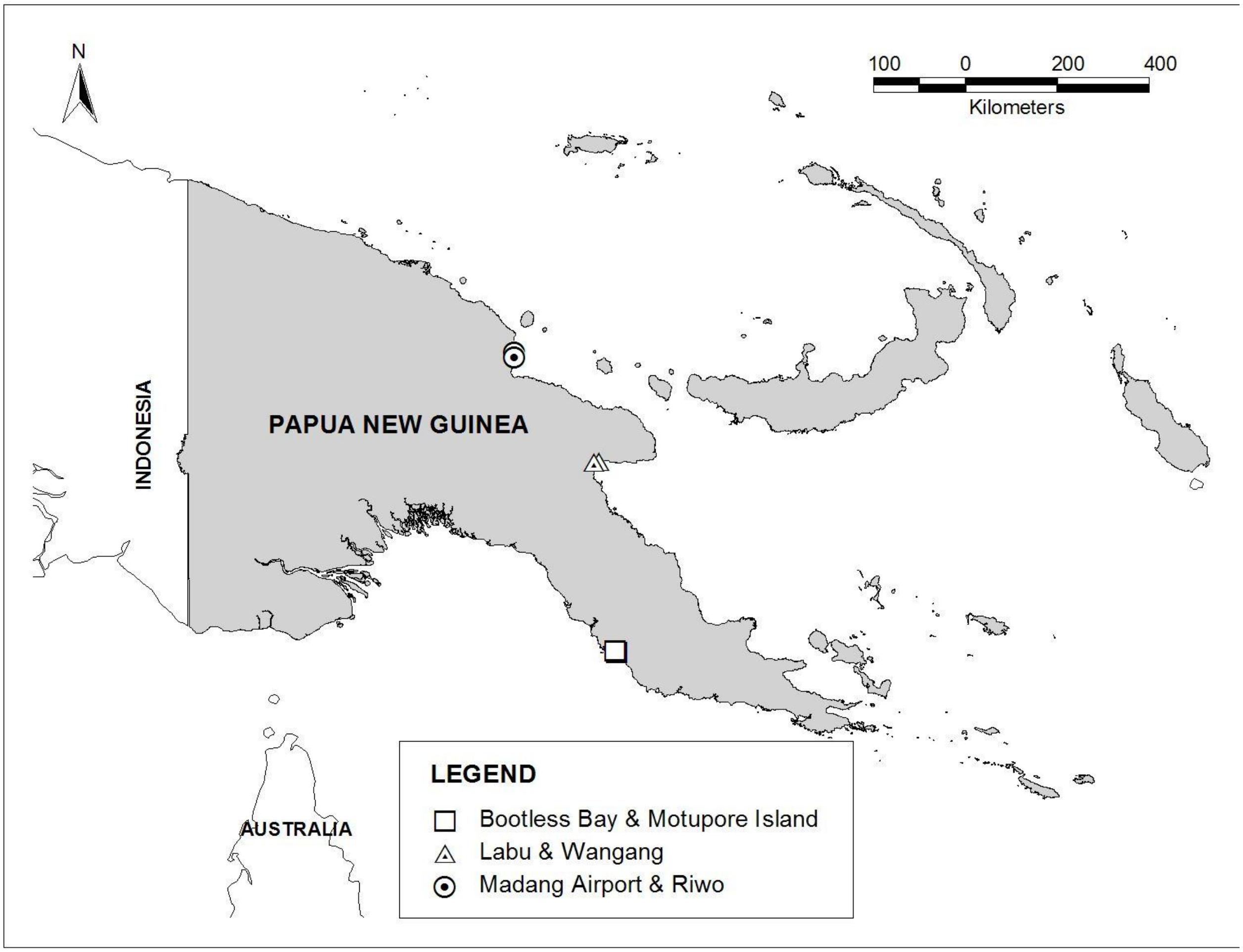

Figure 2.0. Map of the field study sites (Bootless Bay, Motupore Island, Labu, Wangang, Madang airport and Riwo) in Papua New Guinea.

The Labu and Wangang study sites are in the Morobe province, with the latter located ~9 km east of Lae Township at the mouth of Bumbu river by road, and the former site located in the delta of Markham river ~ 6 km by road and sea west of Lae township. Both sites experience similar climatic conditions (McAlpine *et al*. 1983, Table 2.1).

The Riwo and Madang airport study sites are in the Madang province, with the latter located at the fringe of Madang airport, and the former site located ~12 km by road from Madang township. Both sites experience similar climatic conditions (McAlpine *et al*. 1983, Table 2.1).

The four study sites in the northern part of the New Guinea island (Labu, Wangang, Riwo and Madang airport) experience higher monthly precipitation than the two sites (Motupore island and Bootless bay) in the southern part of New Guinea (Table 2.1). Motupore island and Bootless bay mangrove forests receive a mean annual precipitation (MAP) of 1,214 mm, and the Wagang and Labu mangroves in northern side of the island experience a MAP of 4,750 mm and the Riwo and Madang airport mangroves receives about 3,533 mm. Consequently, the northern New Guinea mangroves have much taller and complex canopy (~20 m height) structure similar to adjacent tropical lowland rainforest (Fig.2.3, 2.4). The two mangrove forests in Madang sites displayed similar structural architecture to the Lae sites. The multi-strata canopy communities in northern New Guinea facilitated establishment of rich epiphytic diversity. The Motupore fringe mangrove and Bootless bay communities in contrast have markedly reduced canopy structure (Fig.2.1, 2.2) exhibiting a predominantly single canopy forest structure. Structurally Motupore mangrove community exhibited shorter canopy height (< 8 m height) than the Bootless bay community (generally < 10 m height). The sampled communities display marked variation in species composition both within and between communities. For example, in the Motupore fringe mangrove community, the mean high tide (MLT) zone is colonized by even-height stands of *Aegialitis annulata* merging with *Avicennia marina*, *Sonneratia alba*, and *Rhizophora stylosa*. Whereas, in the neighboring Bootless bay, a potentially dispersal source community to Motupore community had *Rhizophora stylosa* dominating in the MLT zone. The Labu and Wangang mangrove communities had *Rhizophora stylosa* and *Sonneratia alba* dominating the MLT zone and the back swamp mangrove zone (BSM) showed dominance *of Nypha*, *Sonneratia* and *Xylocarpus alba* (Fig. 2.4).

Table 2.1: Coordinates (latitude, longitude), mean annual temperature (MAT), mean annual precipitation in millimeters (MAP), mean percentage relative humidity (%),community type (*sensu* Lugo 1980) of the six different mangrove communities surveyed in this study, number of zones, and number of canopy structure.

Study Site	**Latitude**	**Longitude**	**MAT (^{o}C)**	**MAP (mm)**	**Relative Humidity (%)**	**Community Type**	**Number of Zones**	**Number of Canopy Structure**
Motupore Island	09^{o}31’S	147^{o}17’5E	26.17	1214	67	Island/Fringe mangrove	3	2
Bootless Bay	09^{o}30’S	147^{o}16’E	26.17	1214	67	Riverine mangrove	4	2
Wangang, Lae	06^{o}44’S	147^{o}01’E	25.92	4753	75	Riverine mangrove	4	3

Cont…/

Study Site	**Latitude**	**Longitude**	**MAT (^{o}C)**	**MAP (mm)**	**Relative Humidity (%)**	**Community Type**	**Number of Zones**	**Number of Canopy Structure**
Labu, Lae	06^{o}45’S	146^{o}57’E	25.92	4753	75	Riverine mangrove	4	3
Riwo, Madang	05^{o}08’S	145^{o}47’E	26.46	3533	75	Riverine/Fringe mangrove	4	3
Madang Airport	05^{o}12’S	145^{o}47’E	26.46	3533	75	Fringe mangrove		

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Figure 2.1. Mangrove forest on Motupore island, PNG. In the mean low tide (MLT) zone are *Aegialitis annulata* (dwarf), *Avicennia marina* (silvery green canopy), *Rhizophora stylosa* behind *Aegialitis*. Maximum canopy height is < 6 m define scale in each of these as m

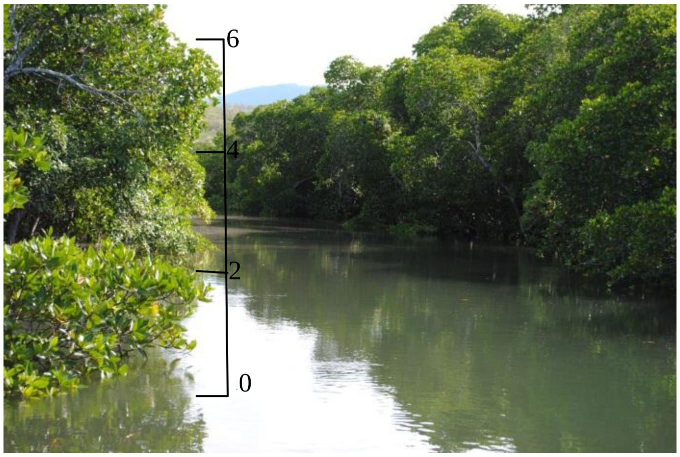


Figure 2.2. Mangrove forest in Bootless bay, PNG. In the MLT zone are *Rhizophora stylosa* (monospecific stand in MLT zone). Showed a maximum canopy height of > 6 > 10 m, with two recognizable canopy layers.

Figure 2.3. Mangrove forest in Wagang, Lae, Morobe Province, PNG. MLT zone). The *Soneratia alba* depicts the characteristic canopy height of > 20 m.

Figure 2.4. Forest in a brackish swamp mangrove (BSM) zone with *Nypa* colonization in Wagang site, PNG. *Nypa* succession into the open water and along the river bank.

Zonation

Mangal systems are commonly categorized into five zones (Watson 1928, Lugo and Snedaker 1974, Percival and Womersly 1975). This classification system is based on a complex of prevailing environmental variables, including periodicity and duration of tides, salinity, terrestrial stream flow, and discontinuities in species' distribution. Existing periodicity and duration of tides appear to be a key factor in mangrove community zonation.

The Bootless Bay mangroves span across ~500 m on either side of a slow flowing creek that drains into Bootless Bay, typifying riverine mangrove characteristics (*sensu* Lugo and Snedaker 1974). The Bootless Bay mangal system displayed three distinct zones typical of most of New Guinea's hyperdiverse mangrove communities (Fig. 2.5b). The stand structures were distinctively shorter than those observed in high rainfall areas (Labu and Riwo mangroves). The Bootless Bay mangal system exhibited an interesting zonation characteristic with the reoccurrence of high salinity species *Avicennia marina* in the rear zone. This pattern was inferred to be a result of increasing salt deposition because of high evaporation in soil surface water and low precipitation. The high salt deposition inhibited establishment of tall tree species thus creating salt flats with high substrate salinity, which favored establishment of high salt tolerant species (e.g. *Avicennia marina*) in the upper high tide (UHT) zone. The mangrove stand along the river exhibited zones of high salt tolerant species in the seafront (low tide zone) and the least salt tolerant species in the back zone. The zonation pattern in mangroves influenced by hinterland rivers such as Bootless Bay becomes more complex with secondary zonation imposed by variation in flood levels.

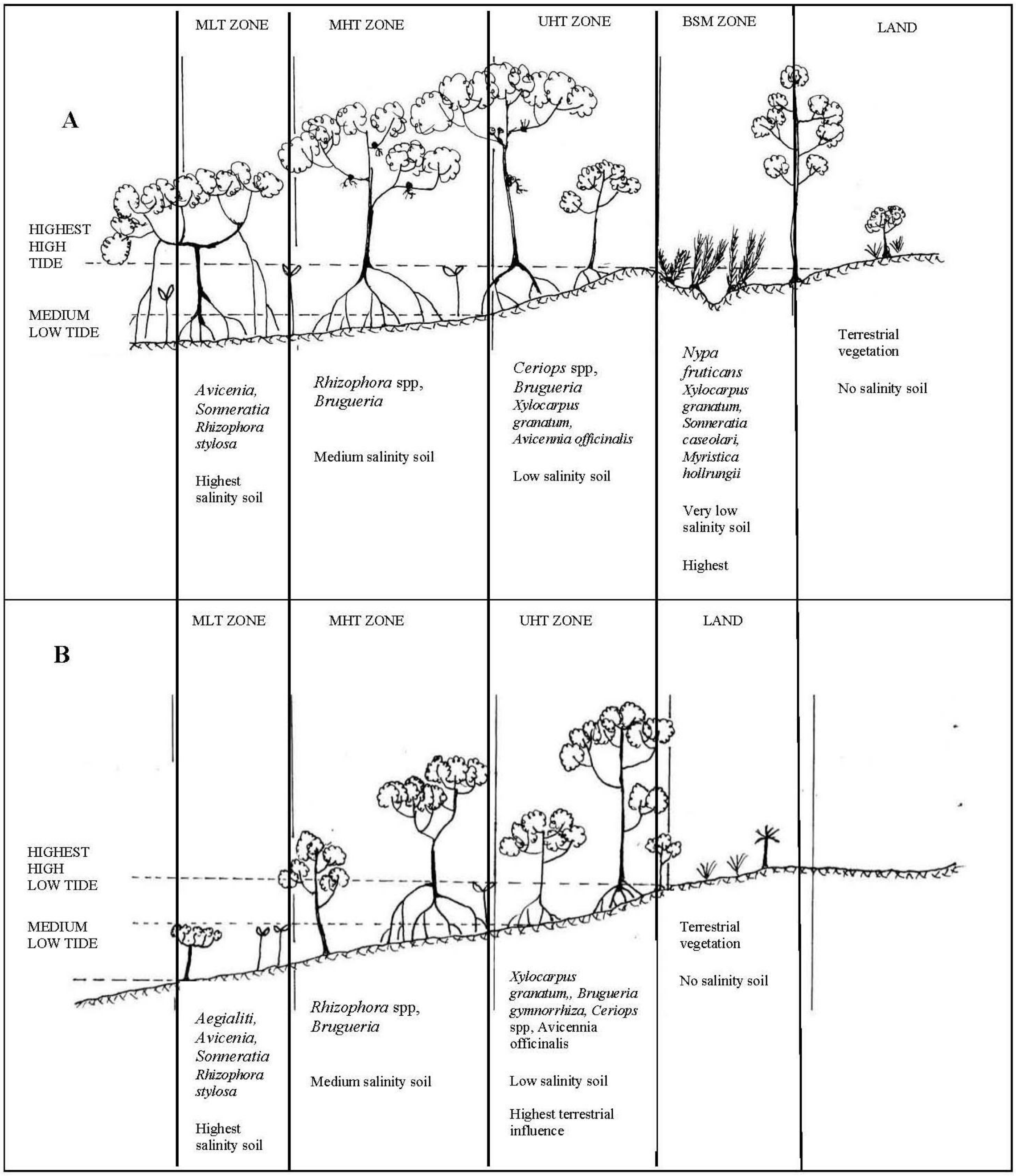


Figure 2.5. Schematic profile diagram of mangrove zonation in Madang and Lae mangrove forest (A) and Bootless Bay and Motupore (B), PNG. The latter sites have three zones; mean low tide (MLT), medium high tide (MHT), and upper high tide (UHT) and the former sites have four zones; MLT, MHT, UHT, and brackish or back swamp mangrove (BSM).

The Motupore Island mangroves, on the other hand, thrive on the fringes of the geological outcrop on the leeward side of the island, which experiences minimal wave and wind actions. The Motupore mangrove community is directly exposed to vertical seawater tidal fluctuation, therefore can be classified a fringe mangroves' category (*sensu* Lugo and Snedaker 1974, Lugo 1980). However, it can also be categorized as an island mangrove due to the small island area effects in which the terrestrial drainage is negligible and salinity stress and nutrient availability predominate (*sensu* Lugo and Snedaker 1974).

The Motupore mangrove displayed three noticeable taxonomic zones or delineation from the seafront toward landward directions with an unnoticeable back zone, namely; *Avicennia-Sonneratia* in the MLT zone, followed by *Rhizophora* in the MHT zone (in areas where *Avicennia* and *Sonnerati*a was missing; *Rhizophora* population extended into the MLT zone, and *Bruguiera-Ceriops-Xylocarpus* in the UHT zone (Fig. 2.5b). In the low tidal zone, spear-head like pneumatophores (adventitious root) extended up to ~50 cm above the substrate, followed by Stilt root, knee-like roots, Plank buttresses, and no buttresses. The Bootless Bay mangal system displayed similar taxonomic delineations, however, with more elaborated spatial distribution patterns and a noticeable back zone.

Mangrove communities in Lae (Wangang and Labu, Table 2.1) and Madang exhibited five zones (Fig. 2.5a). The MLT zone dominated by *Avicennia marina*, *Sonneratia alba*, *Rhizophora stylosa*. The MHT zone was dominated by *Rhizophora* spp, and *Bruguiera gymnorrhiza*. The UHT zone was dominated by *Ceriops* spp, *Xylocarpus granatum*, and *Avicennia officinalis*. The BSM was dominated by *Sonneratia caseolaris*, *Myristica hollrungii*, and *Nypa fruticans*. The species' spatial distribution and structure exhibited a gradient with the shortest species in the most exposed seaward side and increased in canopy height in the landward direction. The shortest canopy height was < 2 m high in *Aegialitis annulata* (Plumbaginaceae), and the maximum was ≤ 5m high in *Bruguiera gymnorrhiza* (Rhizophoraceae). The spatial distribution of species as recognized in their distinct zones is listed in Table 2.2a. The low velocities of incoming and retreating daily tides and well-developed prop root system entrapped vast amounts of organic debris and domestic litter. The high carbon in the mangrove soil therefore is influenced by this entrapment (trapped organic matter).

The Bootless Bay mangroves exhibited taller canopy height than the Motupore community. The shortest stands occurred in the low tide zone with a minimum height of about 3 m in *Rhizophora stylosa* (Rhizophoraceae) and *Avicennia marina* (Acanthaceae). The tallest individuals were up to 8 m occurring in the mid-and back-zones including species such as *Bruguiera gymnorrhiza* (Rhizophoraceae), *Xylocarpus* spp. (Meliaceae), and *Heritiera littoralis* (Sterculiaceae). The mangrove forest floor was mostly open and sparsely covered by saplings of the dominant species. In the sea front where the wave action was highest, sporadic regeneration of *Avicennia marina*, *Sonneratia alba*, and *Aegialitis annulata* were evident within irregular rows of pencil-like pneumatophores of *Sonneratia alba* usually spreading in a radial direction but much denser in the seaward direction. Older trees occasionally had loads of epiphytes such as ant plant, *Hydnophytum* spp. (Rubiaceae), *Myrmecodia* spp. (Rubiacae), orchids *Dendrobium* spp. (Orchidaceae), *Bulbophyllum* spp. (Orchidaceae), ferns (*Asplenium* spp), and mistletoes (*Amyema* spp).

Table 2.2a: Mangrove taxa variation in vein density (D_V, mm mm^{-2}), photosynthetic carbon assimilation rate (A_{max}, µmol CO$_2$m^{-2}s^{-1}), maximum stomatal gas exchange rate (g_{smax}, mmol m^{-2}s^{-1}) across 3 different tidal zones (1, MLT = mean low tide, 2, MHT = medium high tide, 3, UHT = upper high tide).

Family	***Species***	**D_V**	**A_{max}**	**G_{smax}**	**Zone**
Lythraceae	*Aegiceras corniculatum*	9.74 ± 0.45	13.45 ± 0.65	0.15 ± 0.01	1
Sonneratiaceae	*Sonneratia alba*	10.61 ± 1.14	17.44 ± 0.89	0.20 ± 0.01	1
Acanthaceae	*Avicennia marina*	15.24 ± 0.42	19.20 ± 0.88	0.22 ± 0.01	1
Plumbaginaceae	*Aegialitis annulata*	14.02 ± 0.45	17.01 ± 0.89	0.24 ± 0.02	1
Myrtaceae	*Osbornia octodonta*	11.17± 0.79	14.00 ± 0.80	0.24 ± 0.03	1
Mean for MLT Zone		12.16 ± 0.65	16.22 ± 0.82	0.21 ± 0.02	
Median for MLT Zone		11.17± 0.45	17.01 ± 0.88	0.22 ±	
Rhizophoraceae	*Bruguiera gymnorhiza*	7.25± 0.42	9.80 ± 0.35	0.10 ± 0.00	2
Rhizophoraceae	*Rhizophora mucronata*	6.46± 0.30	11.26 ± 0.45	0.12 ±0.02	2
Rhizophoraceae	*Rhizophora apiculata*	8.21± 0.15	12.14 ± 0.65	0.13 ±	2
Rhizophoraceae	*Rhizophora stylosa*	8.56± 1.76	15.77 ± 0.67	0.17 ± 0.02	2
Meliaceae	*Xylocarpus australasicus*	12.33± 0.78	15.86 ± 0.23	0.19 ±0.03	2
Mean for MHT Zone		8.56± 0.68	12.97 ± 0.47	0.14 ±0.02	
Median for MHT Zone		8.21± 0.42	12.14 ± 0.45	0.13 ± 0.02	
Rhizophoraceae	*Ceriops decandra*	6.38± 0.10	7.40 ± 0.20	0.10 ± 0.00	3
Rhizophoraceae	*Ceriops tagal*	6.49± 0.25	7.80 ± 0.22	0.10 ± 0.02	3
Meliaceae	*Xylocarpus granatum*	10.83± 0.87	14.85 ± 0.45	0.18 ± 0.01	3
Acanthaceae	*Acanthus ilicifolius*	4.84± 0.23	4.89 ± 0.23	0.19 ± 0.01	3
Acanthaceae	*Avicennia officinalis*	12.29± 0.43	13.19 ± 0.56	0.22 ± 0.04	3
Mean for UHT Zone		8.17± 0.38	9.63 ± 0.33	0.16 ± 0.02	
Median for UHT Zone		6.49± 0.25	7.80 ±	0.18 ± 0.01	

The Labu and Wangang mangrove communities displayed three recognizable canopy layers (shrub layer, middle story, and main canopy). The Labu and Wangang mangal systems had notable mangrove associates (*Inocarpus* spp, *Instia* spp, *Barringtonia asiatica*, *Hernandia* spp, and *Pongamia* sp). The main canopy was ~30 m height and predominated by five species. Notably, these species were *Cerbera floribunda* (Apocynaceae), *Sonneratia alba* (Sonneratiaceae), *Myristica hollrungii* (Myristicaceae), *Bruguiera gymnorrhiza* (Rhizophoraceae), *Heritiera littoralis* (Sterculiaceae), and *Xylocarpus granatum* (Meliaceae) (Table 2.2). The middle story was dominated by saplings of the main canopy species and mangrove associates. The shrub layer was dominated by *Acorosia* sp, *Mapania* sp, and *Acanthus* sp except for the Labu community where *Nypa fruticans* was prevalent.

The Riwo mangrove system formed a 10 to 200 m wide band of vegetation that buffers the Alexishafen bay coastline. The Madang airport mangal system is part of a narrow band of mangrove that fringes the Madang harbor. The Riwo mangrove exhibited two canopy layers with the main canopy up to 15 m in height; the mangrove was predominated by *Xylocarpus granatum* and *Bruguiera gymnorhiza* in the back-zone. *Rhizophora* spp. dominated the understory, while seedlings of the main canopy species dominated the shrub layer. The Madang airport mangrove community was a largely disturbed community and lacked a well-developed canopy structure. However, it was noticeable that the community was a single congeneric stand of *Avicennia* spp. extending from the MLT zone to the MHT zone.

Leaf structural investigation: Leaf vein density and leaf mass per area

Measurements of leaf vein density (D_V, mm mm^{-2}), leaf mass per area (LMA, g m^{-2}), maximum photosynthesis rate (A_{max}, µmol CO_2 m^{-2}s^{-1}), and maximum stomatal conductance rate (g_{smax}, mmol m^{-2}s^{-1}) were carried out on 31 mangrove species (Appendix 2.3). Leaf mass per area (LMA, g m^{-2}) defined as mean dry mass (g) divided by mean area of plant leaves (m^2) is an emerging leaf trait in understanding the resource-use strategy and relative growth rate in plants (Coley 1988, Poorter and Bongers 2006).

Vein density (D_V) is defined as the mean length of veins (mm) divided by the mean surface area of lamina (Brodribb *et al*. 2007). The D_V trait is the main irrigator of a leaf during photosynthesis and is used as an indicator of net photosynthetic carbon assimilation rate (A_{max}) (Brodribb *et al*. 2007, Noblin *et al*. 2008, Boyce *et al*. 2009, Franks and Beerling 2009, Brodribb and Feild 2010).

Leaf mass per area (LMA)

The leaf samples for the LMA and D_V study were randomly collected from fully expanded undamaged mature leaves from the sun branches of several individuals from the 31 species (Table 2.2b). A sample size of 15 leaves per species was drawn across the species with the exception of *Nypa fruticans* (5 leaves) in this study. The leaves were placed in a zip-lock bag in the field and transported to a nearby field laboratory. I labeled the leaves with a number series for easy accession and scanned them at 300 dpi with the labeled side in view using a portable scanner (Cannon CanoScan LiDe 200, USA). The leaves were then placed in envelopes and oven dried for 2 days at 65^{o}C. The mass of dried leaves (DM, g) was measured with an electronic balance, and the leaf area (LA, m^{-2}) for its corresponding individual leaf measured with ImageJ (version 1.4, NIH, USA). The LMA for a given species was then calculated as a ratio of DM to LA.

Table 2.2b: Checklist of the 31 mangrove species and their corresponding family sampled in this study. Variables; D_V = vein density (mm mm^{-2}), LMA = leaf mass per area (g m^{-3}) and the symbol (+) indicates the trait has been measured for the species.

Family	**Species**	**D_V** (mm mm^{-2})	**LMA** (g m^{-2})
Acanthaceae	*Acanthus ilicifolius*.	+	+
Acanthaceae	*Avicennia alba*	+	+
Acanthaceae	*Avicennia marina* .	+	+
Acanthaceae	*Avicennia officinalis*	+	+
Arecaceae	*Nypa fruticans*	+	+
Bignoniaceae	*Dolichandrone spathacea* .	+	+
Combretaceae	*Luminitzera racemosa*	+	+
Euphorbiaceae	*Excoecaria agallocha*	+	+
Euphorbiaceae	*Rhizophora apiculata*	+	+
Fabaceae	*Cynometra ramiflora*	+	+
Lythraceae	*Aegiceras corniculatum*	+	+
Malvaceae	*Heritiera littoralis*	+	+
Meliaceae	*Xylocarpus australasicus*	+	+
Meliaceae	*Xylocarpus granatum*	+	+
Meliaceae	*Xylocarpus rumphii*	+	+

Cont…/

Family	**Species**	**D_V** (mm mm^{-2})	**LMA** (g m^{-2})
Myristicaceae	*Myristica hollrungii*	+	+
Myrtaceae	*Osbornia octodonta*	+	+
Plumbaginaceae	*Aegilitis annulata*	+	+
Plumbaginaceae	*Pemphis acidula*	+	+
Rhizophoraceae	*Bruguiera cylindrica*	+	+
Rhizophoraceae	*Bruguiera exaristata*	+	+
Rhizophoraceae	*Bruguiera gymnorrhiza*	+	+
Rhizophoraceae	*Bruguiera parviflora*	+	+
Rhizophoraceae	*Ceriops decandra*	+	+
Rhizophoraceae	*Ceriops tagal*	+	+
Rhizophoraceae	*Rhizophora mucronata*	+	+
Rhizophoraceae	*Rhizophora stylosa*	+	+
Rhizophoraceae	*Scyphiphora hydrophyllacea*	+	+
Rubiaceae	*Bruguiera sexangula*	+	+
Sonneratiaceae	*Sonneratia alba*	+	+
Stemonuraceae	*Stemonurus apicalis*	+	+

Leaf vein density (D_V)

Leaf samples for D_V were collected from the same sun branches from which the samples for LMA were collected throughout the six study sites. Five fully expanded undamaged mature leaves from five different plants were collected from 31 species. The leaf samples were placed in falcon tubes and stored in ethanol (80%) until measurements. Because mangroves have succulent leaves, which resist the standard leaf clearing method (Boyce *et al.* 2009), modification of the Boyce *et al*. (2009) protocol (described hereafter) was necessary for the mangrove leaves. Leaf samples from ethanol were rinsed with water, and three tissue sections (each *c*. 3 cm^2) located well away from the mid-vein and margin were cut out using a fresh double-edged razor blade for clearing. To speed the clearing process, each leaf tissue had the cuticle scratched (~0.1 mm deep) in the adaxial (upper) side with a fresh double-edged razor blade. The tissue sections were then placed on a Petri dish with the sliced side facing downward and immersed in 10% bleach to a level at which the whole leaf tissue was totally submerged. Heat (65^oC) was then applied using hot plate under constant observation until the scratched spots in the tissue turned into a white translucent color. Heat was then removed, and the tissue was allowed to cool at room temperature for 10 minutes. The leaf tissue was then rinsed in tap water and stained with either safranin at room temperature for three minutes or in a boiling Toluidine Blue ‘O’ for 10 seconds for vein staining. At the end of staining, the leaf tissue was rinsed with clean cold water using a disposable polyethylene transfer pipette until all excess stain was removed. The leaf tissue was then imbedded on a microscope slide mounted with a thin film of glycerin jelly on a hot plate (40^oC) and pressed with a cover slip. I then placed the mounted slide on a level surface and added sizeable weight (nut) on the cover slip to evenly spread the gel over the tissue and allowed the gel to dry at room temperature. The cleared leaf tissue was then imaged with a digital camera (Nikon D3000 VR) at 5-10x using an upright microscope (Trinocular Microscope T490B). For each leaf tissue, three images of different areas of the cleared tissue were taken. I then transferred the digital images to a laptop computer (Dell Studio 1537) and measured the vein lengths using ImageJ software (version 1.4; NIH Image, Bethesda, MD, USA). Five measurements of D_V were made from a minimum of three leaves from three individuals of each species. The taxon D_V was obtained by averaging the five vein length measurements (Brodribb *et al*. 2007, Boyce *et al*. 2009).

Leaf gas exchange measurements

Leaf photosynthetic rates (A_{max}, µmol CO_2 m^{-2} s^{-1}) and maximal stomatal conductance (g_{smax}, mmol H_2O $m^{-2}s^{-1}$) under saturating light (1800 to 2200 mmol m^{-2} s^{-1}, set to match full sun conditions in the field) and optimal conditions of water availability were measured using an open gas exchange analyzer (Li-6400XT, Licor Biosciences, Lincoln, Nebraska, USA). Leaf temperatures were in the range of 27 to 33 ºC, CO_2 at 380 μmol mol^{-1}, and VPD (vapour pressure deficit) was maintained < 1.3 kPa. CO_2 was controlled by trapping ambient air with a plastic bag and attaching it to the input port to the infrared gas analyzer. The bag was protected from sunlight to prevent large swings in chamber humidity. Excess humidity was scrubbed using fresh Drierite in the desiccant column. Mean instantaneous rates of A_{max} were calculated from 10 leaves collected from three to five individual plants between 0900 h and 1100 h (Brodribb *et* *al*. 2007, Feild *et al*. 2011a). Measurements of A_{max} and g_{smax} under these physiologically optimal conditions were taken as the maximum for each species (Brodribb *et al*. 2007).

Ecological characterization of zonation, growth forms, and leaf salt balance

The five notable zones include the following in my study sites: Zone 1: The highly exposed mangrove (HEM) zone is an area occupied by species that thrive successfully on a highly exposed seaward side and inundated during all high tides. This zone is typically dominated by *Avicennia marina, Sonneratia alba, Aegialitis annulata, Rhizophora stylosa* and *R.mucronata*. Zone 2: The medium exposed mangrove (MEM) zone is occupied by less dynamic, exposed seaward sides, inundated by all medium high tides. This zone is typically co-dominated by *Sonneratia alba* and *Avicennia alba.* Zone 3: The central mangrove (CM) zone is inundated by a normal high tide and occurs between the seaward and landward bands. The zone is shared by a number of species (*Rhizophora* spp, *Bruguiera* spp. and *Xylocarpus* spp) and is considered as the real climax zone (Giesen *et al*. 2007). Zone 4: The back mangrove zone (BM) is inundated by all spring tides and occurs in the rear end of mangrove distribution. This zone is commonly occupied by *Excoecaria agallocha, Nypa fruticans, Lumnitzera racemosa, Xylocarpus moluccensis*, and *Pandanus tectora* (Giesen *et al*. 2007). Zone 5: brackish stream mangroves (BSM) zone consists of bands of mangroves that occur along brackish to almost pure fresh water streams, which may be occasionally inundated by exceptionally high tides. This zone is predominated by *Sonneratia caseolaris, Cerbera* spp, *Gluta velutina, Xylocarpus granatum, Myristica hollrungii,* and *Nypa fruticans* (Percival and Womersley 1975).

The boundaries between the above five zones are often very fine and virtually inseparable in field grading. Thus, I collapsed the five into four zones based on an easily visible parameter such as species' exposure to different daily high tides. Notably, these four zones included the following: HEM or Zone 1 was "mean low tide" (MLT). Zone 2 (MEM) and Zone 3(CM) were grouped together to represent a "medium high tide" (MHT) zone. Zone 4 (BM) was re-labeled as upper high tide (UHT) zone and zone 5 (BSM) constituted zone 4. The back swamp mangrove is noticeable in mangrove formations associated with perennial rivers.

Mangrove species were grouped into three major categories of salt excretion modes (salt excretion, salt accumulation, and ultrafiltration, i.e. excluding salt at the root level to keep it from entering the transpiration stream.) In the field survey, all encountered mangrove species were first categorized as being either salt secretors (salt excreted through leaves) or non-salt secretors. Salt secreting mangroves were identified through visible observation and tasting the salt crystals on the leaves. Next, the non-salt secretors were further divided into salt accumulators and salt exclusion (ultrafiltration) (Tomlinson 1986) and rooting types. It was observed that different excretion modes showed an appreciable relationship with rooting types (Appendix 2.1).

Individuals were also grouped into three recognizable growth forms (shrub, small-medium tree, and large tree) based on mature stand height classes. Individuals with mature stem structure and well-developed secondary branches with predominant height of < 3 m were grouped as shrubs. Individuals > 3 m and < 5 m were classified as small to medium trees, and those > 5 m were classified as large trees (Raunkiaer 1934).

Statistical analyses

I normalized the data and used one-way analysis of variance (ANOVA) to test for statistically significant differences in A_{max}, g_{smax} ,LMA, and D_V among the different zones (MLT, MHT and UHT) and plant growth forms (shrub, small-medium tree, large tree) (Fordyce *per comm*. 2011). For group and treatment data that showed significant one-way ANOVA F-test, I used a pairwise multiple comparison (PMC) procedure (Holm-Sidak method) to explore the nature of these group and treatment differences. Relationships among leaf traits (i.e., A_{max}, g_{smax}, D_V, LMA) zonation (reflecting biogeophysiochemical environmental gradient), and growth forms were analyzed using linear regression analysis. Simple correlation and linear regression were used to test for a relationship between the following: g_{smax} versus D_V, A_{max} versus D_V, and LMA versus D_V using Sigmaplot 11 systat software.

RESULTS

Photosynthetic gas exchange in relation to zonation, and growth forms

Photosynthetic gas exchange traits (A_{max}, µmol CO_2 $m^{-2}s^{-1}$ and g_{smax}, mmol H_2O $m^{-2}s^{-1}$) varied among different zones and growth forms (Fig. 2.6, 2.7, Table 2.2, 2.4). A_{max} varied by about four-fold across species within each zone and ranged from 13.45 ± 0.65 SD µmol CO_2 m^-

$^{2}s^{-1}$ in *Aegiceras corniculatum* to19.02 ± 0.88 SD µmol CO_2 $m^{-2}s^{-1}$ in *Avicennia marina* for the MLT zone, 9.8 ± 0.35 SD µmol CO_2 m^{-2} s^{-1} in *Bruguiera gymnorrhiza* to 15.86 ± 0.23 SD µmol $CO_2m^{-2}s^{-1}$ in *Xylocarpus australasicus* for the MHT zone, and 6.49 ± 0.25 SD µmol CO_2 $m^{-2}s^{-1}$ in *Ceriops tagal* to 14.85 ± 0.45 SD µmol CO_2 $m^{-2}s^{-1}$ in *Xylocarpus granatum* for the UHT zone. Among different zones, A_{max} varied by about seven-fold across species within the zones (Fig. 2.8). The MLT zone ranged from 14.00 ± 0.8 SD µmol CO_2 $m^{-2}s^{-1}$ in *Osbornia octodonta* to 19.02 ± 0.88 SD µmol CO_2 $m^{-2}s^{-1}$ in *Avicennia marina*. The MHT zone ranged from 4.89 ± 0.23 SD µmol CO_2 $m^{-2}s^{-1}$ in *Acanthus ilicifolius* to 15.86 ± 0.23 SD µmol CO_2 $m^{-2}s^{-1}$ in *Xylocarpus australasicus*. The UHT zone ranged from 7.40 ± 0.25 SD µmol CO_2 $m^{-2}s^{-1}$ in *Ceriops decandra* to 14.85 ± 0.45 SD µmol CO_2 $m^{-2}s^{-1}$ in *Xylocarpus granatum* (Table 2.3).

The ANOVA showed significant differences in A_{max} among zones and growth forms ($F_{2,12} = 3.89$, $P < 0.05$) and ($F_{2,12} = 4.69$, $P < 0.05$) respectively. A pairwise multiple comparison (PMC) procedure (Holm-Sidak method) was used to explore the nature of these zone differences. The PMC showed that A_{max} of zone 1 versus zone 3 had a significantly higher ($P < 0.02$) mean difference. The mean differences of zone 2 versus zone 3 and zone 1 versus zone 2 were not significantly different ($P>0.05$) (Table 2.3). The PMC showed A_{max} of growth form 3 versus growth form 2 had significantly higher ($P <0.01$) mean difference. The mean differences of growth form 1 versus growth form 2 and growth from 3 versus growth form 1 were not significantly different.

The g_{smax} values for different zones and plant growth forms varied markedly between the three zones. The g_{smax} for the MLT zone ranged from 0.19 ± 0.02 SD mmol H_2O $m^{-2}s^{-1}$ in *Sonneratia alba* to 0.24 ± 0.01 SD mmol $m^{-2}s^{-1}$ in *Osbornia octodonta*; MHT ranged from 0.10 ±0.01 SD mmol H_2O $m^{-2}s^{-1}$ in *Bruguiera gymnorrhiza* to 0.18 ± 0.01 SD in *Acanthus ilicifolius;*

and UHT ranged from 0.10 ± 0.003 SD mmol H_2O $m^{-2}s^{-1}$ in *Ceriops tagal* to 0.22 ± 0.03 SD mmol $m^{-2}s^{-1}$ in *Avicennia officinalis* (Fig. 2.8 Table 2.4). The g_{smax} showed marked differences between the three different growth forms (Fig. 2.9). The g_{smax} ranged from 0.16 ± 0.02 SD mmol H_2O $m^{-2}s^{-1}$ in *Aegiceras corniculatum* to 0.24 ± 0.01 SD mmol H_2O $m^{-2}s^{-1}$ in *Osbornia octodonta* for shrubs, 0.10 ± 0.03 SD mmol $m^{-2}s^{-1}$ in *Ceriops tagal* to 0.20 ± 0.03 SD in *Ceriops decandra* for small-medium trees, and 0.10 ±*.02* SD mmol H_2O $m^{-2}s^{-1}$ in *Xylocarpus australasicus* to 0.23 ± 0.03 SD mmol H_2O $m^{-2}s^{-1}$ in *Avicennia marina* for large trees. ANOVAs on mean g_{smax} differences among different zones and plant growth forms showed significant differences among the zones ($F_{2,15} = 4.20$, $P < 0.04$) and the plant growth forms ($F_{2,9} = 5.75$, $P < 0.03$)(Table 2.3). Given that the one-way ANOVA F-test showed statistically significant differences in g_{smax} among the three zones and three growth forms. A pairwise multiple comparison (PMC) procedure (Holm-Sidak method) was used to explore the nature of these zone differences. The PMC showed that g_{smax} of zone 1 versus zone 2 had a significantly ($P < 0.02$) higher mean difference. The mean differences of zone 1 versus zone 3 and zone 3 versus zone 2 were not significantly different (Table 2.3). The PMC showed g_{smax} of growth form 3 versus growth form 2 had significantly ($P < 0.01$) higher mean difference. The mean differences of growth form 1 versus growth form 2 and growth from 3 versus growth form 1 were not significantly different.

Table 2.3: The Fishers test (F-test) and the pairwise multiple comparison (PMC) procedure (Holm-Sidak method) results. Abbreviation A_{max} = maximum photosynthetic carbon assimilation, Zone 1 = mean low tide zone, Zone 2 = medium high tide zone, Zone 3 = upper high tide zone, DM = difference of means, p= unadjusted P, Yes = significant difference, No = no significant difference, P = probability value, t = t test statistics, F-test = ANOVA F-test value, and P-value = corresponding probability level, LMA = leaf mass per area, D_V = vein density, grwthF1 = growth form 1, grwthF2 = growth form 2, grwthF3 = growth form 3. Growth form 1, 2, and 3 refer to shrub, small-medium tree, large tree respectively. Ultrafilt = ultrafilter (exclude salt from entering the root), Accummul = salt accumulator (accumulate salt in tissue), and Excretion = excrete salt from leaf.

Comparison	**DM**	**p**	**t**	**P < 0.05**	**F-test**	**P-value**
A_{max}zone1 vs. A_{max}zone3	5.45	0.02	2.77	Yes	$F_{2,12}$=3.89	0.05
A_{max}zone1 vs. A_{max}zone2	3.27	0.12	1.66	No		
A_{max}zone2 vs. A_{max}zone3	2.19	0.29	1.11	No		
A_{max}gwthF3 vs. A_{max}grwthF2	7.07	0.012	3.04	Yes	$F_{2,10}$=4.69	0.04
A_{max}gwthF1 vs. A_{max}grwthF2	4.713	0.084	1.922	No		
A_{max}gwthF3 vs. A_{max}grwthF1	2.358	0.335	1.014	No		
g_{smax}zone1 vs. g_{smax}zone2	0.08	0.01	2.9	Yes	$F_{2,15}$=4.20	0.04
g_{smax}zone1 vs. g_{smax}zone3	0.04	0.14	1.55	No		
g_{smax}zone3 vs. g_{smax}zone2	0.04	0.2	1.34	No		
g_{smax}grwthF3 vs. g_{smax}grwthF2	0.113	0.011	3.181	Yes	$F_{2,9}$=5.75	0.03

Comparison	**DM**	**p**	**t**	**P < 0.05**	**F-test**	**P-value**
g_{smax}grwthF1 vs. g_{smax}grwthF2	0.093	0.028	2.61	No		
g_{smax}grwthF3 vs. g_{smax}grwthF1	0.02	0.583	0.57	No		
LMAzone1 vs. LMAzone3	91.495	0.001	4.43	Yes	$F_{2,10}$=9.89	0.004
LMAzone2 vs. LMAzone3	58.067	0.024	2.667	Yes		
LMAzone1 vs. LMAzone2	33.428	0.137	1.618	No		
D_V zone1 vs. D_V zone2	3.536	0.014	2.753	Yes	$F_{2,17}$=3.83	0.04
D_V zone1 vs. D_V zone3	2.207	0.104	1.718	No		
D_V zone3 vs. D_V zone2	1.329	0.297	1.077	No		
D_V grwthF3 vs. D_V grwthF1	3.009	0.001	3.84	Yes	$F_{2,18}$=7.55	0.004
D_V grwthF2 vs. D_V grwthF1	1.909	0.025	2.436	No		
D_V grwthF3 vs. D_V grwthF2	1.1	0.177	1.404	No		
Ultrafilt vs. Accumul	50.577	<0.001	3.886	Yes	F2,20=8.81	0.002
Excretion vs. Accumul	44.036	0.004	3.269	Yes		
Ultrafilt vs. Excretion	6.541	0.633	0.486	No		

Relations of leaf mass per area, zonation, and plant growth form

The LMA (g m^{-3}) varied markedly among different zones (Fig. 2.11, Table 2.5), with ~two-fold difference in the MLT zone, ranging from 161.91 ± 12.45 SD g m^{-3}in *Aegiceras corniculatum* to 289 ± 10.12 SD g m^{-3} in *Pemphis acidula*, with a mean of 209.52 ± 7.89 SD g m^{-3}. In the MHT zone, LMA varied by ~two-fold, ranging from 107.45 ± 5.6 SD g m^{-3} in *Excoecaria agallocha* to 232.09 ± 8.98 SD g m^{-3} in *Rhizophora stylosa*, with a mean of 162.57 ± 9.15 g m^{-3}. In the UHT zone, LMA varied by about two-fold, ranging from 106.13 ± 7.80 SD g m^{-3}in *Dolichandrone spathacea* to 212.68 ± 3.42 SD g m^{-3}in *Nypa fruticans*, with a mean of 160.65 ± 8.09 g m^{-3}, and in the BSM zone, LMA ranged from 93.14 ± 7.32 g m^{-3} in *Bruguiera cylindrica* to 117.67 ± 9.89 g m^{-3} in *Stemonurus apiccalis*, with a mean of 129.38 ± 6.29 g m^{-3}. An ANOVA testing the differences in LMA among the different zones was highly significant ($F_{2,10} = 9.89$, $P < 0.004$). Because the one-way ANOVA F-test showed statistically significant differences in LMA among the three zones and three growth forms, it necessitate the use of a pairwise multiple comparison (PMC) procedure (Holm-Sidak method) to establish the nature of these zone differences. The PMC showed that LMA of zone 1 versus zone 3 and zone 2 versus zone 3 both had significantly ($P < 0.05$) higher mean differences. The mean differences of zone 1 versus zone 2 were not significantly different (Table 2.3).

LMA across different plant growth forms showed variation between growth forms (Fig. 2.12, Table 2.5). LMA within the shrubby growth form ranged from 109.32 ± 7.81 SD g m^{-3} to 289.00 ± 10.12 SD g m^{-3} with a mean of 186.13 ± 8.13 SD g m^{-3}; small-medium trees ranged from 107.45 ± 5.6 SD g m^{-3} to 190.69 ± 6.20 SD g m^{-3} and mean of 169.48 ± 7.43 SD g m^{-3} large trees ranged from 93.14 ± 7.30 SD g m^{-3} to 232.09 ± 8.98 SD g m^{-3} and mean of 150.91 ± 8.69 SD g m^{-3}, and the only palm mangrove was 211.00 ± 3.42 SD g m^{-3}. However, an ANOVA among the three plant growth forms showed that the mean differences in terms of LMA were not statistically significant ($F_{2,17} = 1.43$, $P > 0.05$).

Relationship between vein density (D_V), zonation and growth forms

The D_V (mm mm^{-2}) of species among different zones varied markedly (Fig. 2.13). It varied by ~ two-fold in the MLT zone, ranging from 6.89 ± 0.78 SD mm mm^{-2} in *Pemphis acidula* to 15.23 ± 0.42 SD mm mm^{-2} in *Avicennia marina*); by ~two-fold in the MHT zone, ranging from 4.84 ± 0.23 SD mm mm^{-2} in *Acanthus ilicifolius* to 12.33 ± 0.78 mm mm^{-2} in *Xylocarpus australasicus*; by ~ two-fold in the UHT zone, ranging from 6.38 ± 0.102 SD mm mm^{-2} in *Ceriops decandra* to 12.72 ± 0.78 SD mm mm^{-2} in *Xylocarpus rumphii*; and by ~ two-fold in the BSM zone, ranging from 4.93 ± 0.38 SD mm mm^{-2} in *Stemonurus apicalis* to 8.53 ± 0.19 SD mm mm^{-2} in *Cynometra ramiflora*. An ANOVA to test the significance of mean differences in D_V among the three different zones was significant ($F_{2,15}= 4.12$, $P < 0.04$). Because the one-way ANOVA F-test showed statistically significant differences in D_V among the three zones, a pairwise multiple comparison (PMC) procedure (Holm-Sidak method) was used to explore the nature of these zone differences. The PMC showed that D_V of zone 1 versus zone 2 had a significantly ($P < 0.05$) higher mean difference. The mean differences of zone 1 versus zone 3 and zone 3 versus zone 2 were not significantly different (Table 2.3).

Examination of D_V versus growth form showed variation among plant growth forms (Fig. 2.14). D_V varied by ~ three-fold in shrubs, ranging from 4.84 ± 0.23 SD in *Acanthus ilicifolius* to 14.02 ± 0.45 in *Aegilitis annulata*), by ~ two-fold in small to medium trees, ranging from 8.50 ± 0.45 in *Ceriops decandra* to 14.02 ± 0.45 in *Bruguiera exaristata*), and by ~ three-fold in large trees, ranging from 4.93 ± 0.34 *Stemonurus apicalis* to 15.24 ± 0.42 in *Avicennia marina*. An ANOVA on test on the significance of mean differences in D_V among the three different growth forms was highly significant ($F_{2,18} = 7.55$, $P < 0.04$). Because the one-way ANOVA F-test showed statistically significant differences in D_V among the three growth forms, a PMC post hoc procedure (Holm-Sidak method) was used to establish where the differences were among the contrasting growth forms. This showed that D_V of growth form 3 versus growth form 1 had a significantly ($P < 0.05$) higher mean difference. The mean differences of growth form 2 versus growth form 1 and growth form 3 versus growth from 2 were not significantly different (Table 2.3).

Relationships among leaf mass per area, vein density, and salt excretion modes

A linear regression analysis of light-saturated net CO_2 assimilation rate (A_{max}) against D_V for 31 species (Fig. 2.15) displayed a highly significant regression ($y = 0.946x + 4.289$, $R^2 = 0.68$, $P < 0.001$) indicating a strong link between D_V (mm mm^{-2}) and Amax (µmol $CO_2 m^{-2} s^{-1}$). Linear regression analysis of maximum stomatal conductance also showed a highly significant regression ($y = 0.00568x + 8.095$, $R^2 = 0.79$, $P < 0.001$) indicating a strong relationship between

D_V (mm mm^{-2}) and g_{smax} (mmol m^{-2}s^{-1}) (Fig. 2.16). A regression analysis of D_V and LMA for 31 co-occurring mangrove species showed no evidence of a relationship between the two leaf traits ($R^2 = 0.01$, $P > 0.05$) (Fig. 2.17).

LMA varied among different salt excretions modes (Fig. 2.18). The LMA for salt accumulators varied dramatically, ranging from 94.02 ± 4.53 SD g m^{-2} in *Cynometra ramiflora* to 289.00 ± 10.12 SD g m^{-2} in *Pemphis acidula*. The salt excretors, ranged from 117.43 ± 6.34 SD g m^{-2} in *Acanthus ilicifolius* to 176.23 ± 5.67 SD g m^{-2} in *Avicennia officinalis*. The ultrafiltration species varied dramatically, ranging from 93.14 ± 7.32 SD g m^{-2} in *Bruguiera cylindrica* to 232.09 ± 8.98 SD g m^{-2} in *Rhizophora stylosa*. An ANOVA on test on the significance of mean differences in LMA among the three different salt secretory modes (SEM) was highly significant ($F_{2,20} = 8.81$, $P < 0.002$). Given that the one-way ANOVA F-test showed statistically significant differences in LMA among the three SEM. A pairwise multiple comparison (PMC) procedure (Holm-Sidak method) was used to explore the nature of these zone differences. The PMC showed that LMA of ultrafiltors versus zone accumulators and excretors versus accumulators were significantly ($P < 0.05$) higher mean difference. The mean difference of ultrafiltors versus excretors was not significantly different (Table 2.3).

Distribution of species with different salt secretion modes

Examination of relative abundance of different salt secretion modes across the 31 species indicated 41.94% are salt accumulators, 19.35% are salt excretors, and 38.71% are ultrafilters (Fig. 2.19, appendix 2.1).

Table 2.4: Variation in vein density (D_V, µm mm^{-2}), photosynthetic carbon assimilation rate (A_{max}, µmol $CO_2 m^{-2} s^{-1}$), maximum stomatal gas exchange rate (g_{smax}, mmol $m^{-2} s^{-1}$) across three growth forms (shrub, small-medium tree, large tree as defined in the Materials and Methods) for 31 species of New Guinea mangroves.

Family	**Species**	**D_V**	**A_{max}**	**g_{smax}**	**Growth Form**
Acanthaceae	*Acanthus ilicifolius*	4.84 ± 0.23	4.89 ± 0.23	0.19 ± 0.01	1
Lythraceae	*Aegiceras corniculatum*	9.74 ± 0.45	13.45 ± 0.65	0.15 ± 0.01	1
Myrtaceae	*Osbornia octodonta*	11.17 ±0.79	14 ± 0.8	0.24 ± 0.03	1
Plumbaginaceae	*Aegilitis annulata*	14.02 ± 0.45	17.01 ± 0.89	0.24 ± 0.02	1
Mean for shrub growth form		9.94 ± 0.48	12.34±	0.20 ± .02	
Median for shrub growth form		10.46 ± 0.45	13.73±	0.21 ± .02	
Rhizophoraceae	*Ceriops decandra*	6.38 ± 0.10	7.4 ± 0.2	0.1 ± 0	2
Rhizophoraceae	*Ceriops tagal*	6.49 ± 0.25	7.8 ± 0.22	0.1 ± 0.02	2
Mean for small-medium tree growth form		6.44 ± 0.18	7.60 ± 21	0.10 ± 0.01	

Cont…/

Family	**Species**	**D_V**	**A_{max}**	**g_{smax}**	**Growth Form**
Median for small-medium tree growth form		6.44 ± 0.18	7.60 ±23	0.10 ± 0.01	
Rhizophoraceae	*Rhizophora mucronata*	6.46 ± 0.30	11.26 ± 0.45	0.12 ± 0.02	3
Rhizophoraceae	*Brugueria gymnorhiza*	7.25 ± 29	9.8 ± 0.35	0.1 ± 0	3
Rhizophoraceae	*Rhizophora apiculata*	8.21 ± 0.15	12.14 ± 0.65	0.13 ± 0.02	3
Rhizophoraceae	*Rhizophora stylosa*	8.56 ± 1.76	15.77 ± 0.67	0.17 ± 0.02	3
Sonneratiaceae	*Sonneratia alba*	10.61 ± 1.14	17.44 ± 0.89	0.2 ± 0.01	3
Meliaceae	*Xylocarpus granatum*	10.83 ± 0.87	14.85 ± 0.45	0.18 ± 0.01	3
Acanthaceae	*Avicennia officinalis*	12.29 ± 0.43	13.19 ± 0.56	0.22 ± 0.04	3
Meliaceae	*Xylocarpus australasicus*	12.33 ± 0.78	15.86 ± 0.23	0.19 ± 0.03	3
Acanthaceae	*Avicennia marina*	15.24 ± 0.42	19.2 ± 0.88	0.22 ± 0.01	3
Mean for large tree growth form		10.20 ± 0.70	14.39 ± 38	0.17 ± 0.02	
Median for large tree growth form		10.61 ± 0.43	14.85 ± 35	0.18 ± 0.02	

Table 2.5: The minimum, maximum, and mean leaf mass per area (LMA, g m^{-2}) across the zonation and plant growth forms. The abbreviations MLT = mean low tide, MHT = medium high tide, UHT = upper high tide and BSM = back swamp mangrove zone. Three growth forms (shrub, small-medium tree, large tree as defined in the Materials and Methods)

	Leaf Mass per Area (LMA)		
Zonation	Minimum	Maximum	Mean
MLT	161.91±12.45	289.00±10.12	209.52±7.89
MHT	107.45±5.60	232.09±8.987	162.57±9.15
UHT	106.13±7.80	212.68±3.42	160.65±8.09
BSM	93.14±7.32	117.67±9.89	129.38±6.29
Growth Form			
Shrub	109.32±7.81	289.00±10.12	186.13±8.13
Small-medium trees	107.45±5.60	190.69±6.20	169.48±7.45
Large trees	93.14±7.320	232.09±8.98	150.91±8.69

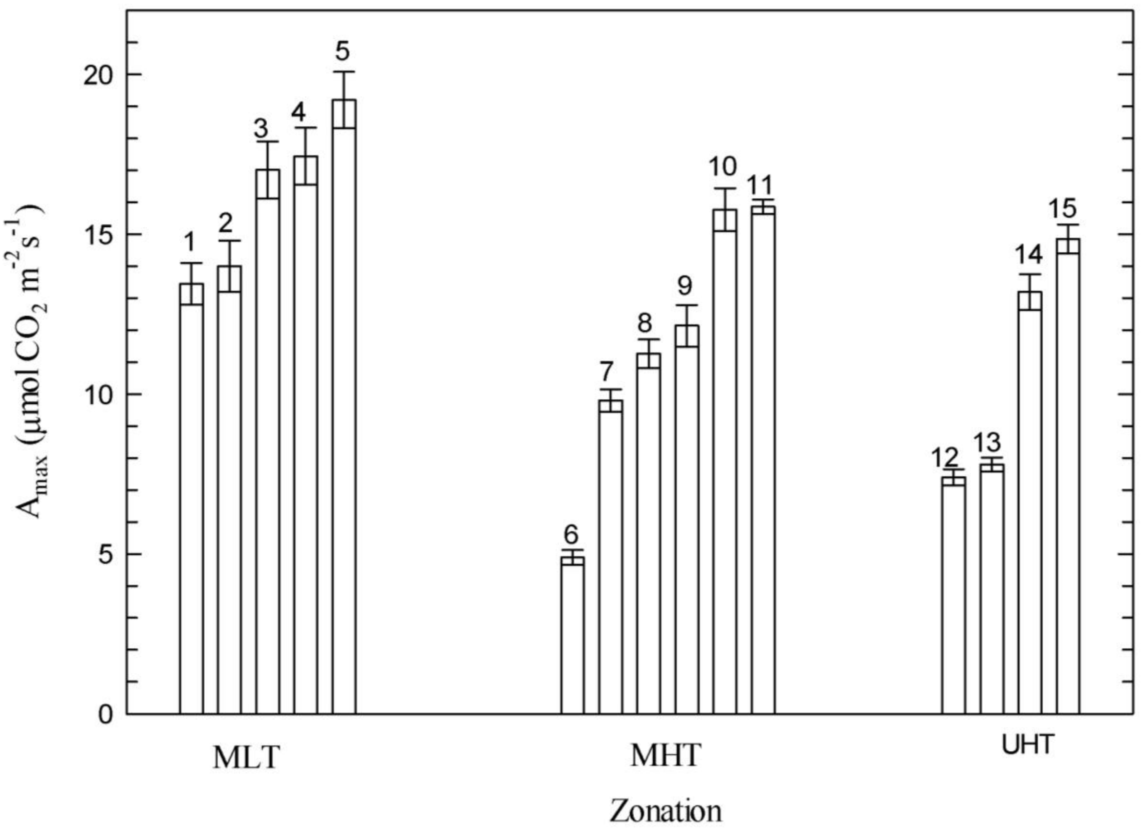


Figure 2.6. Variation in A_{max} across community zonations (MLT = Mean Low Tide, MHT = Medium High Tide, UHT = Upper High Tide) in 15 species of New Guinea mangroves. Data points are means of five samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: *1=Aegiceras corniculatum, 2=Osbornia octodonta*, 3=*Aegialitis annulata, 4=Sonneratia alba, 5=Avicennia marina, 6=Acanthus ilicifolius*, 7=*Bruguiera gymnorhiza, 8=Rhizophora mucronata. 9=Rhizophora apiculata, 10=Rhizophora stylosa, 11=Xylocarpus australasicus, 12=Ceriops decandra, 13=Ceriops tagal, 14=Avicennia officinalis, 15=Xylocarpus granatum.*

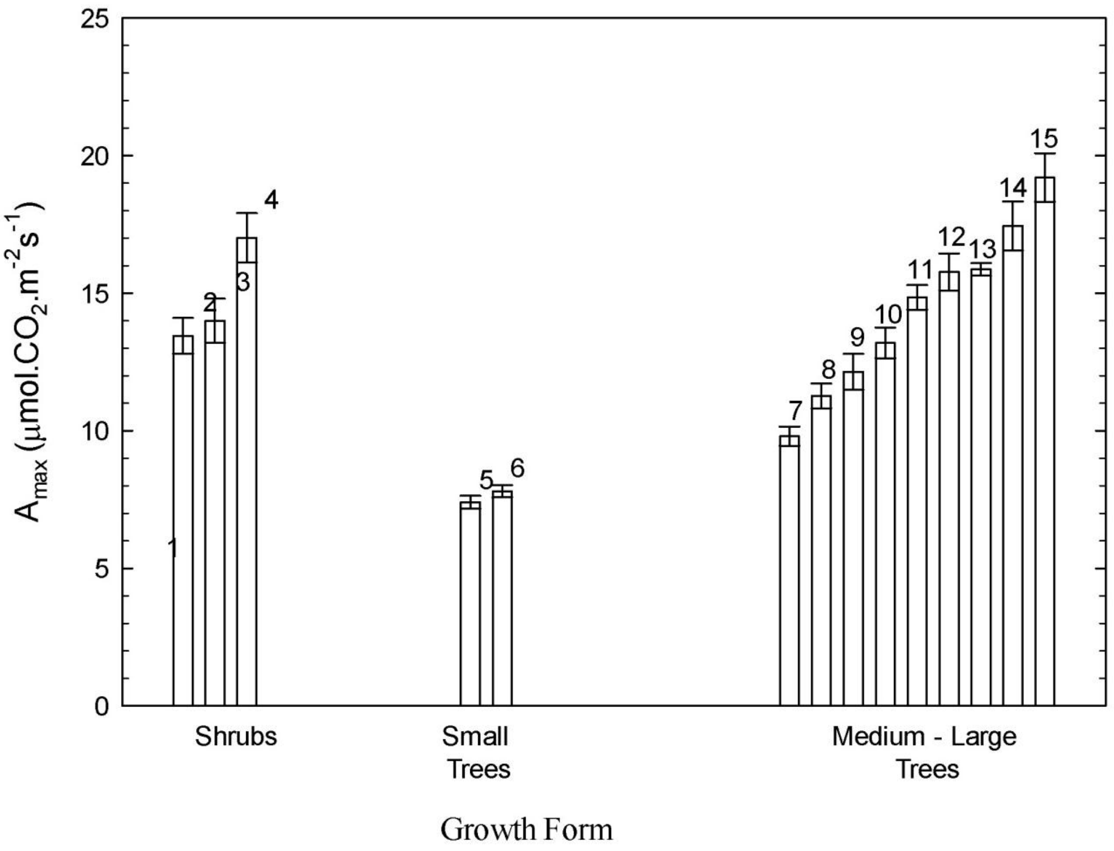


Figure 2.7. Variation of A_{max} among growth forms (Shrubs, Small Trees, Medium-Large Trees) in 15 species of New Guinea mangroves. Data points are means with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: *1=Acanthus ilicifolius, 2=Aegiceras corniculatum,* 3=*Osbornia octodonta*, 4=*Aegialitis annulata, 5= Ceriops decandra, 6=Ceriops tagal, 7=Bruguiera gymnorrhiza, 8=Rhizophora mucronata, 9=Rhizophora apiculata, 10=Avicennia officinalis, 11=Xylocarpus granatum, 12=Rhizophora stylosa, 13=Xylocarpus australasicus, 14=Sonneratia alba, 15=Avicennia marina.*

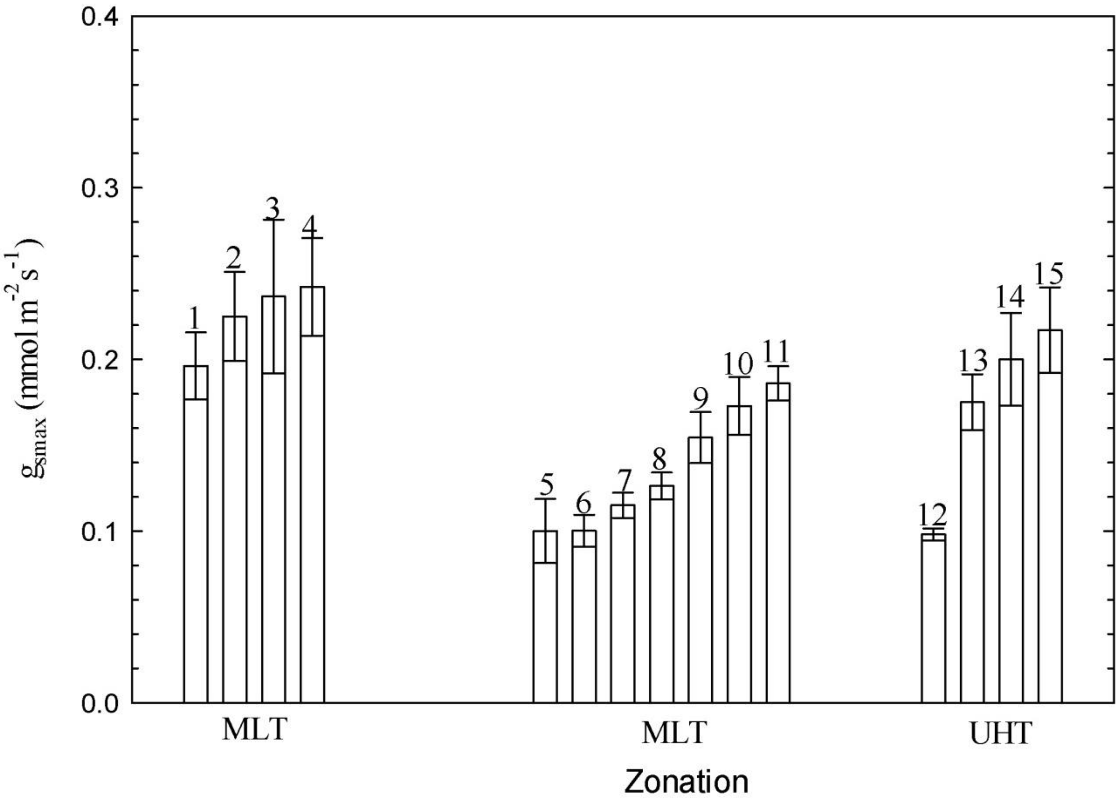


Figure 2.8. Variation of g_{smax} (mmol m^{-2}s^{-1}) among mangrove zones (MLT= Mean Low Tide, MHT=Medium High Tide, UHT=Upper High Tide). Data points are means of sample size of *n* = 10 except for species 1 and 4 where *n* = 8, with error bars denoting the standard deviation around the mean: 1=*Osbornia octodonta*, 2=*Aegilitis annulata*, 3=*Sonneratia alba*, 4=*Avicennia marina*, 5=*Acanthus ilicifolius,* 6= *Bruguiera gymnorrhiza*, 7=*Rhizophora mucronata*, 8=*Rhizophora apiculata*, 9=*Aegiceras corniculatum*, 10=*Rhizophora stylosa*, 11=*Xylocarpus australasicus*, 12=*Ceriops decandra*, 13=*Ceriops tagal*, 14=*Avicennia officinalis*, 15=*Xylocarpus granatum*.

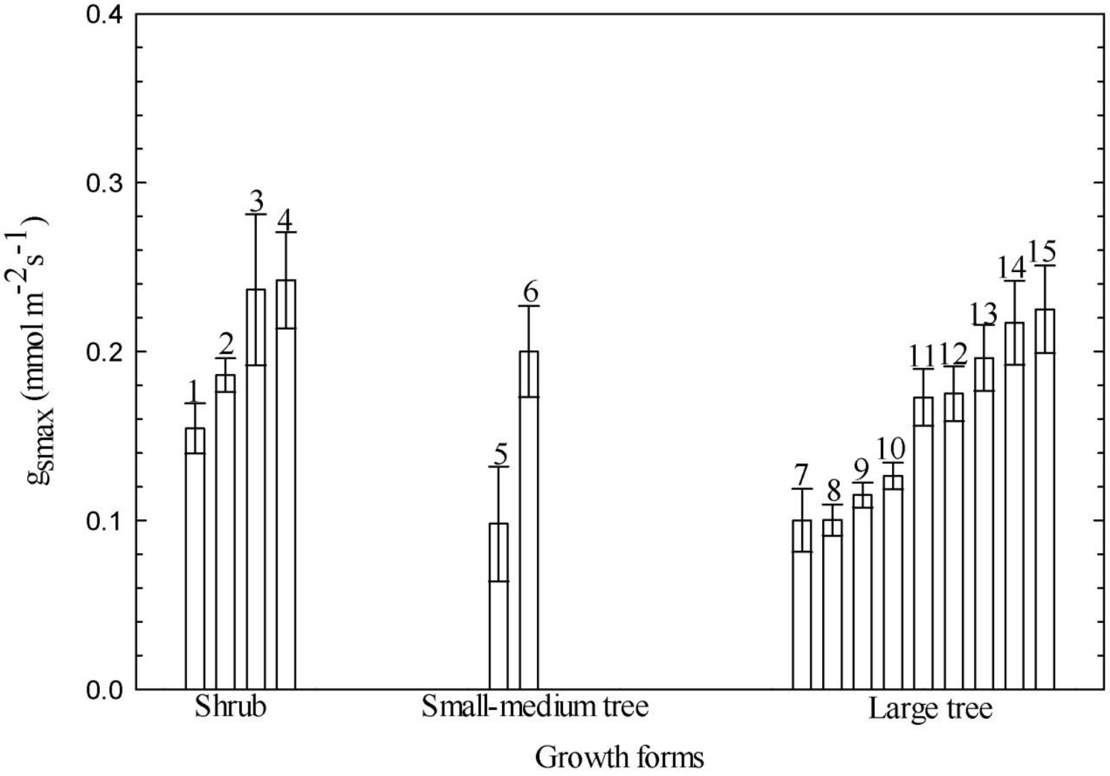
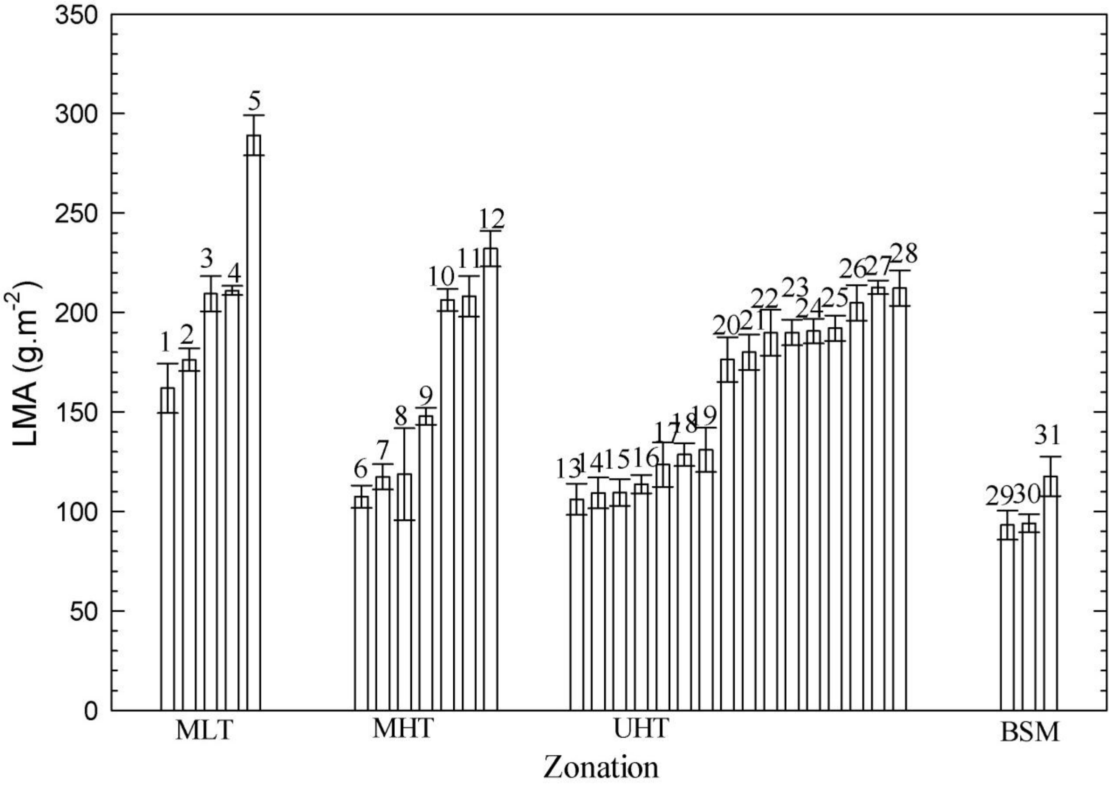


Figure 2.9. Variation of g_{smax} (mmol m^{-2}s^{-1}) among three different growth forms. Data points are means of sample size of *n* = 10 except for species 1 and 4 where *n* = 8, with error bars denoting the standard deviation around the mean: 1=*Aegiceras corniculatum*, 2=*Acanthus ilicifolius*, 3=*Aegilitis annulata*, 4=*Osbornia octodonta*, 5=*Ceriops tagal*, 6=*Ceriops decandra*, 7=*Xylocarpus australasicus*, 8=*Bruguiera gymnorrhiza*, 9=*Rhizophora mucronata*, 10=*Rhizophora apiculata*, 11=*Rhizophora stylosa*, 12=*Xylocarpus granatum*, 13=*Sonneratia alba*,14=*Avicennia officinalis*,15=*Avicennia marina*.

Figure 2.11. Variation in LMA across 31 species and zonation (MLT, MHT, UHT, BSM). Data points are means of sample size of *n* = 10 with error bars denoting the standard deviation around the mean: 1=*Aegiceras corniculatum*, 2=*Avicennia marina*, 3=*Aegialitis annulata*, 4=*Osbornia octodonta*, 5=*Pemphis acidula*, 6=*Excoecaria agallocha*, 7=*Acanthus ilicifolius*, 8=*Xylocarpus australasicus*, 9=*Rhizophora mucronata*, 10=*Bruguiera gymnorhiza*, 11=Rhizophora apiculata, 12=*Rhizophora stylosa*, 13=*Dolichandrone spathacea*, 14=*Scyphiphora hydrophyllacea*, 15=*Xylocarpus rumphii*, 16=*Xylocarpus granatum*, 17=*Bruguiera parviflora*, 18=*Avicennia alba*, 19=*Bruguiera sexangula*, 20=*Avicennia officinalis*, 21=*Myristica hollrungii*, 22=*Ceriops decandra*, 23=*Ceriops tagal*, 24=*Bruguiera exaristata*, 25=*Heritiera littoralis*, 26=*Luminitzera racemosa*, 27=*Sonneratia alba*, 28=*Nypa fruticans*, 29=*Bruguiera cylindrica*, 30=*Cynometra ramiflora*, 31=*Stemonurus apicalis*.



350
300
250
200
150
100
50
0
LMA (g.m^{-2})
1
2
3
4
5
6
7
8
9
10
11
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15
16
17
18
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21
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24
25
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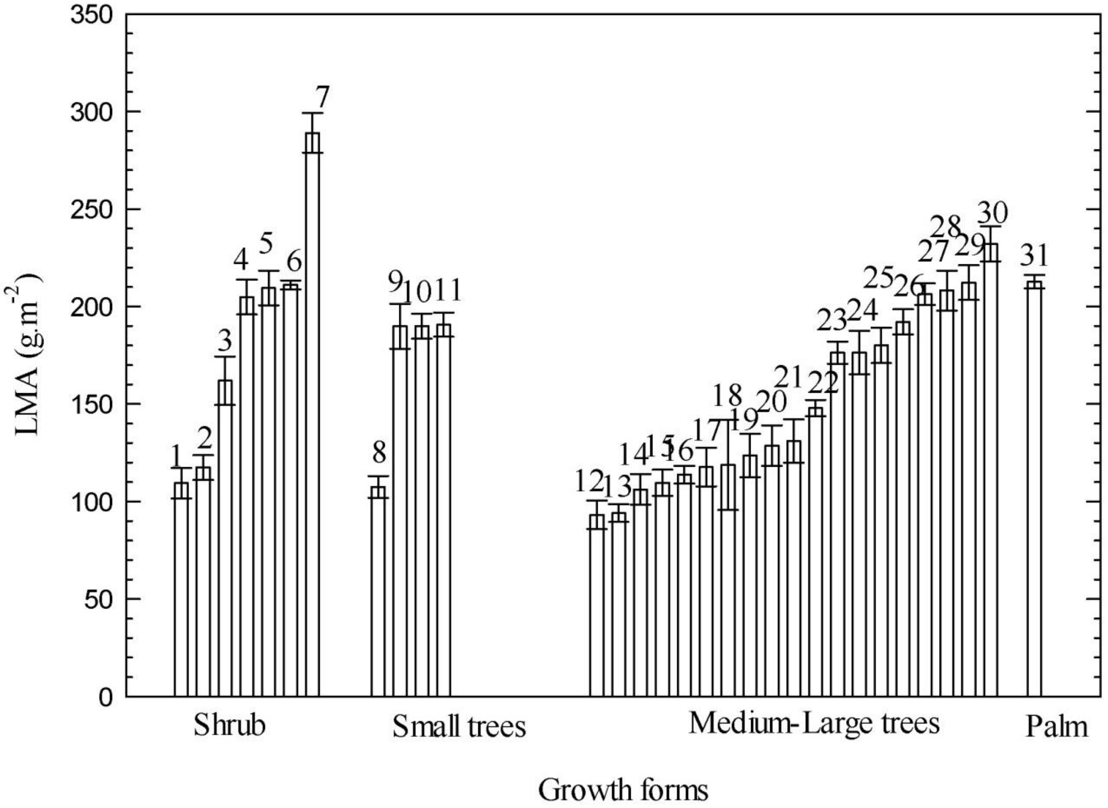
27
28
29
30
31
MLT
MHT
UHT
BSM
Zonation

Figure 2.11.

Figure 2.12. Variation of LMA (g.m^{-2}) among plant growth forms. Data points are means of sample size n = 10, with error bars denoting the standard deviation around the mean. 1=*Scyphiphora hydrophyllacea*, 2=*Acanthus ilicifolius*, 3=*Aegiceras corniculatum*, 4=*Luminitzera racemosa*, 5=*Aegialitis annulata*, 6=*Osbornia octodonta*, 7=*Pemphis acidula*, 8=*Excoecaria agallocha*, 9= *Ceriops decandra*, 10=*Ceriops tagal*, 11=*Bruguiera exaristata*, 12=*Bruguiera cylindrica*, 13=*Cynometra ramiflora*, 14=*Dolichandrone spathacea*, 15=*Xylocarpus rumphii*, 16=*Xylocarpus granatum*, 17=*Stemonurus apicalis*, 18=*Xylocarpus australasicus*, 19=*Bruguiera parviflora*, 20=*Avicennia alba*, 21=*Bruguiera sexangula*, 22=*Rhizophora mucronata*, 23=*Avicennia marina*, 24=*Avicennia officinalis*, 25=*Myristica hollrungii*, 26=*Heritiera littoralis*, 27=*Bruguiera gymnorhiza*, 28=*Rhizophora apiculata*, 29=*Sonneratia alba*, 30=*Rhizophora stylosa*, 31=*Nypa fruticans*.


350
300
250
200
150
100
50
0
LMA (g.m^{-2})
1
2
3
4
5
6
7
8
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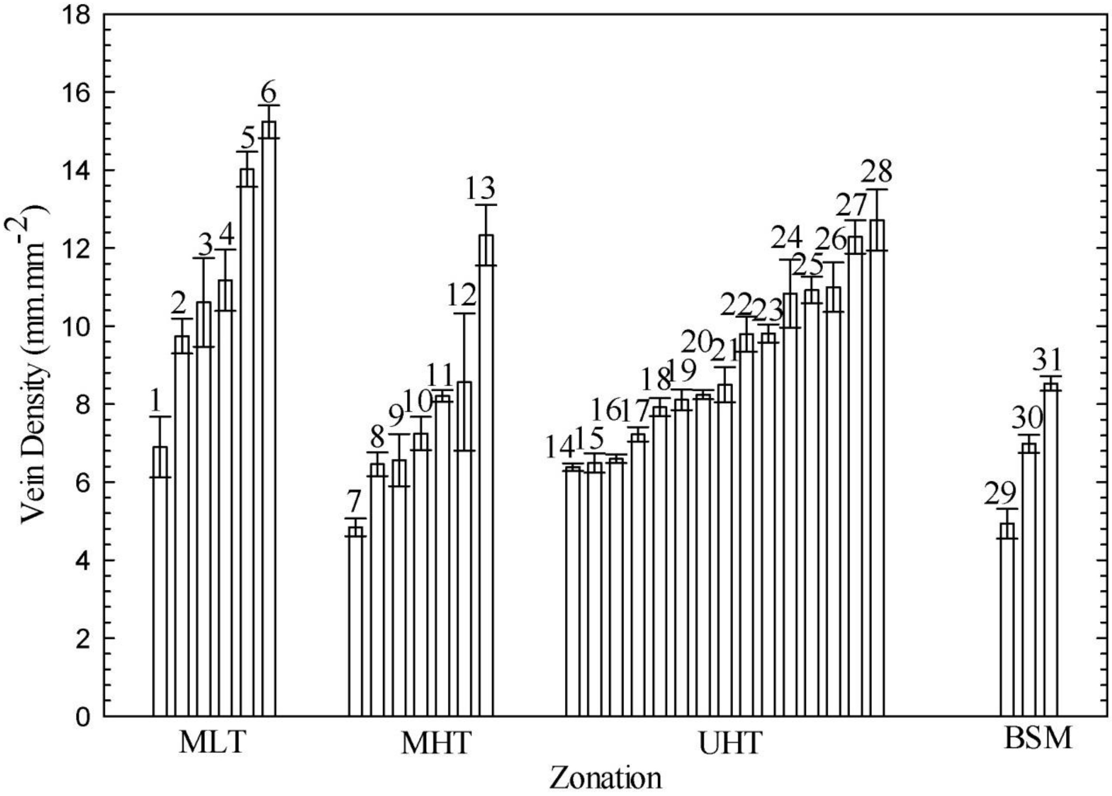
22
23
24
25
26
27
28
29
30
31
Shrub
Small trees
Medium-Large trees
Palm
Growth forms

Figure 2.12.

Figure 2.13. Variation in vein density (mm mm^{-2}) among different zones. Data points are means of sample size n = 10, with error bars denoting the standard deviation around the mean. 1=*Pemphis acidula*, 2=*Aegiceras corniculatum*, 3=*Sonneratia alba*, 4=*Osbornia octodonta*, 5=*Aegialitis annulata*, 6=*Avicennia marina,* 7=*Acanthus ilicifolius,* 8=*Rhizophora mucronata*, 9=*Excoecaria agallocha*, 10=*Bruguiera gymnorrhiza*, 11=*Rhizophora apiculata*, 12=*Rhizophora stylosa*, 13=*Xylocarpus australasicus,* 14= *Ceriops decandra*, 15=*Ceriops tagal*, 16=*Bruguiera sexangula*, 17=*Bruguiera parviflora*, 18=*Luminitzera racemosa*, 19=*Heritiera littoralis,* 20=*Scyphiphora hydrophyllacea*, 21=*Bruguiera exaristata*, 22=*Avicennia alba*, 23=*Nypa fruticans*, 24=*Xylocarpus granatum*, 25=*Dolichandrone spathacea*, 26=*Myristica hollrungii,* 27=*Avicennia officinalis*, 28=*Xylocarpus rumphii*, 29=*Stemonurus apicalis*, 30=*Bruguiera cylindrica*, 31=*Cynometra ramiflora*.


Vein Density (mm.mm^{-2})
18
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
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28
29
30
31
MLT
MHT
UHT
BSM
Zonation

Figure 2.13.

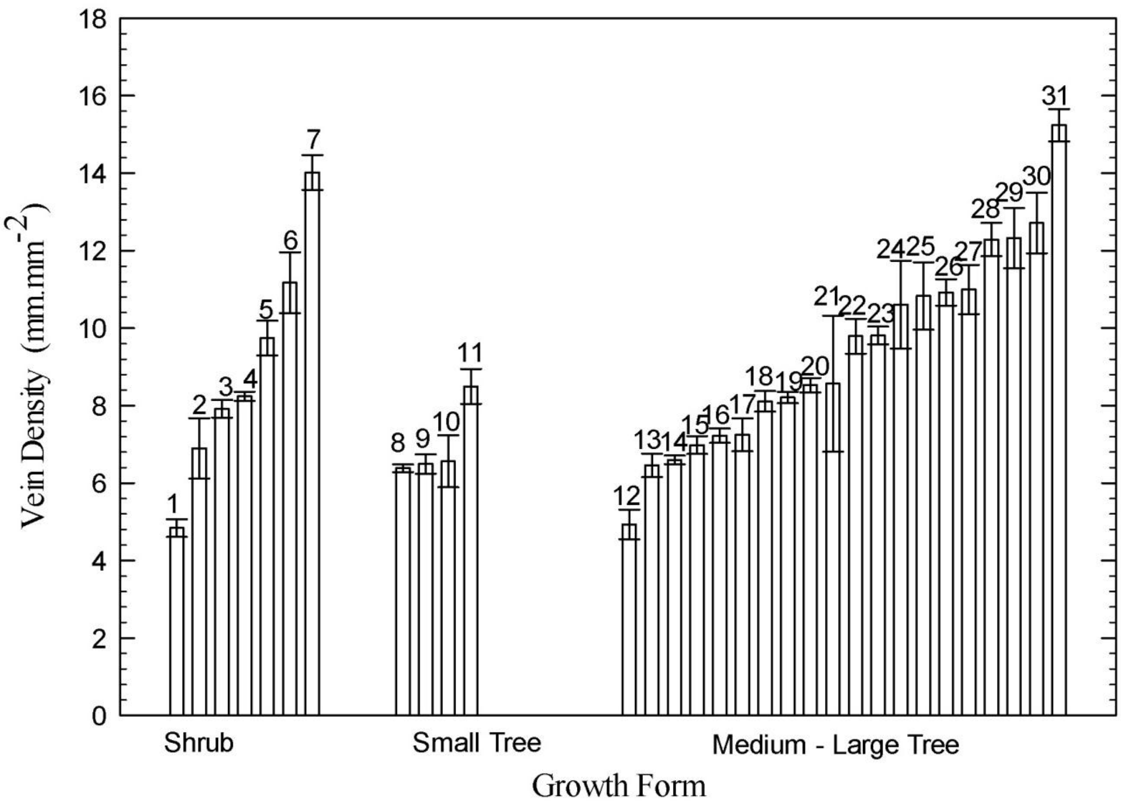


Figure 2.14. Variation of vein density with growth forms. Data points are means of sample size *n* = 10, with error bars denoting the standard deviation around the mean. 1=*Acanthus ilicifolius*, 2=*Pemphis acidula*, 3=*Luminitzera racemosa*, 4=*Scyphiphora hydrophyllacea*, 5=*Aegiceras corniculatum*, 6=*Osbornia octodonta*, 7=*Aegialitis annulata*, 8=*Ceriops decandra*, 9=*Ceriops tagal*, 10=*Excoecaria agallocha*, 11=*Bruguiera exaristata*, 12=*Stemonurus apicalis*, 13=*Rhizophora mucronata*, 14=*Bruguiera sexangula*, 15=*Bruguiera cylindrica*, 16=*Bruguiera parviflora*, 17=*Bruguiera gymnorrhiza*, 18=*Heritiera littoralis*, 19=*Rhizophora apiculata*, 20=*Cynometra ramiflora*, 21=*Rhizophora stylosa*, 22=*Avicennia alba*, 23=*Nypa fruticans*, 24=*Sonneratia alba*, 25=*Xylocarpus granatum*, 26=*Dolichandrone spathacea*, 27=*Myristica hollrungii*, 28=*Avicennia officinalis*, 29=*Xylocarpus australasicus*, 30=*Xylocarpus rumphii*, 31=*Avicennia marina.*

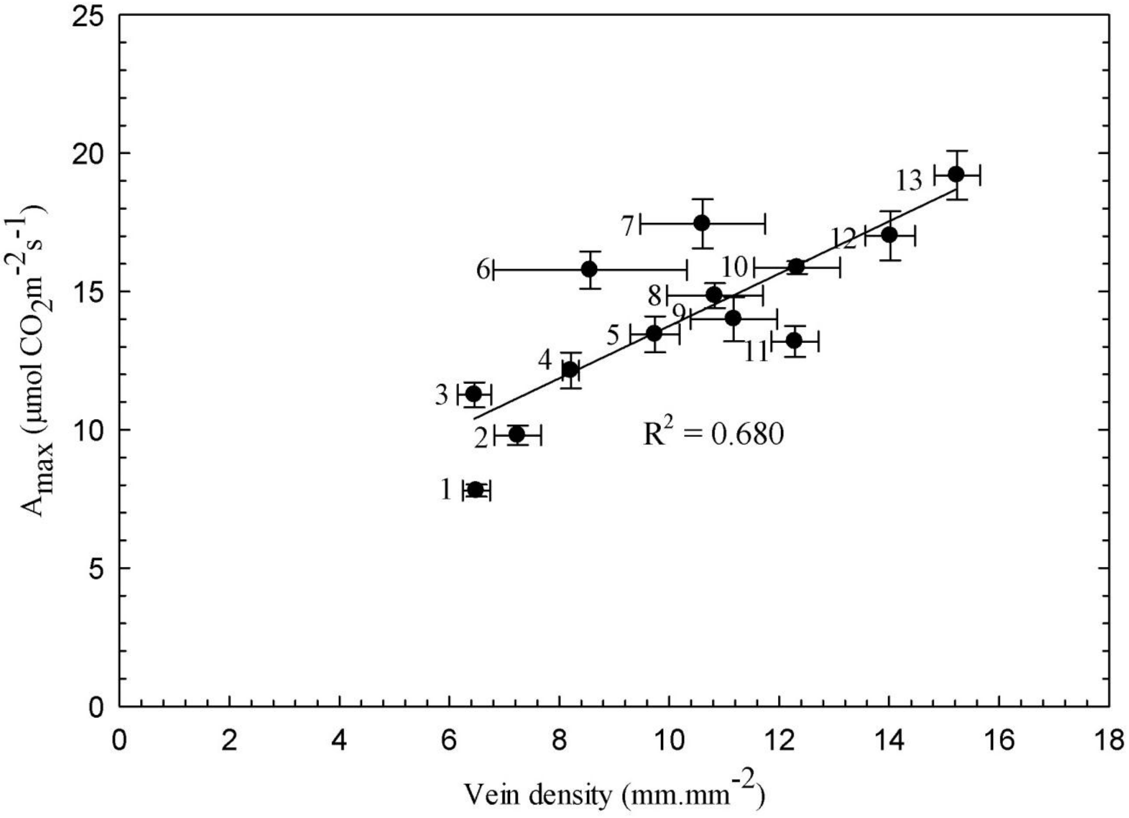


Figure 2.15. Correlation between A_{max} (µmol CO_2 $m^{-2}s^{-1}$) and vein density (mm mm^{-2}) in leaves of 13 common mangrove species: 1=*Ceriops tagal*, 2=*Bruguiera gymnorrhiza*, 3=*Rhizophora mucronata*, 4=*Rhizophora apiculata*, 5=*Aegiceras corniculatum*, 6=*Rhizophora stylosa*, 7=*Sonneratia alba*, 8=*Xylocarpus granatum*, 9=*Osbornia octodonta*, 10=*Xylocarpus australasicus*, 11=*Avicennia officinalis*, 12=*Aegialitis annulata*, 13=*Avicennia marinaAvicennia marina*. Symbols denote means with SES (n = 10). A highly significant regression ($y = 0.946x + 4.289$, $R^2= 0.68$, $P < 0.001$) indicated a strong correlation between D_V (mm mm^{-2}) and A_{max} (µmol CO_2 $m^{-2}s^{-1}$.)

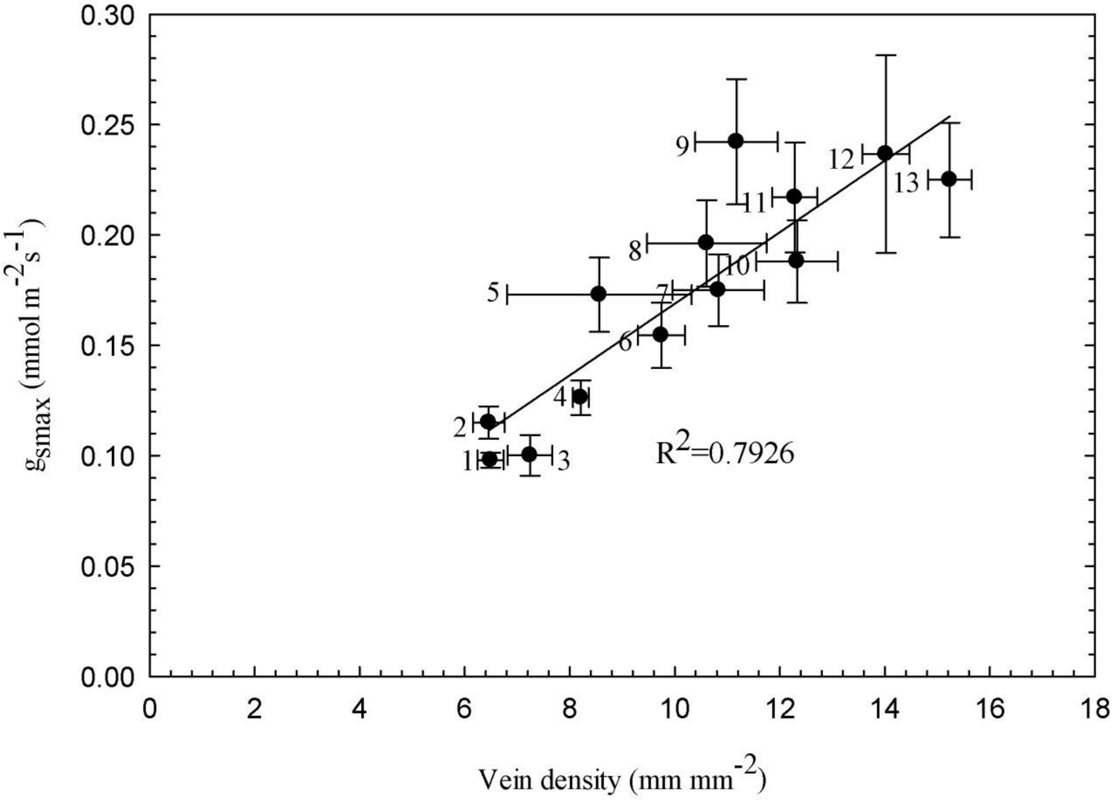
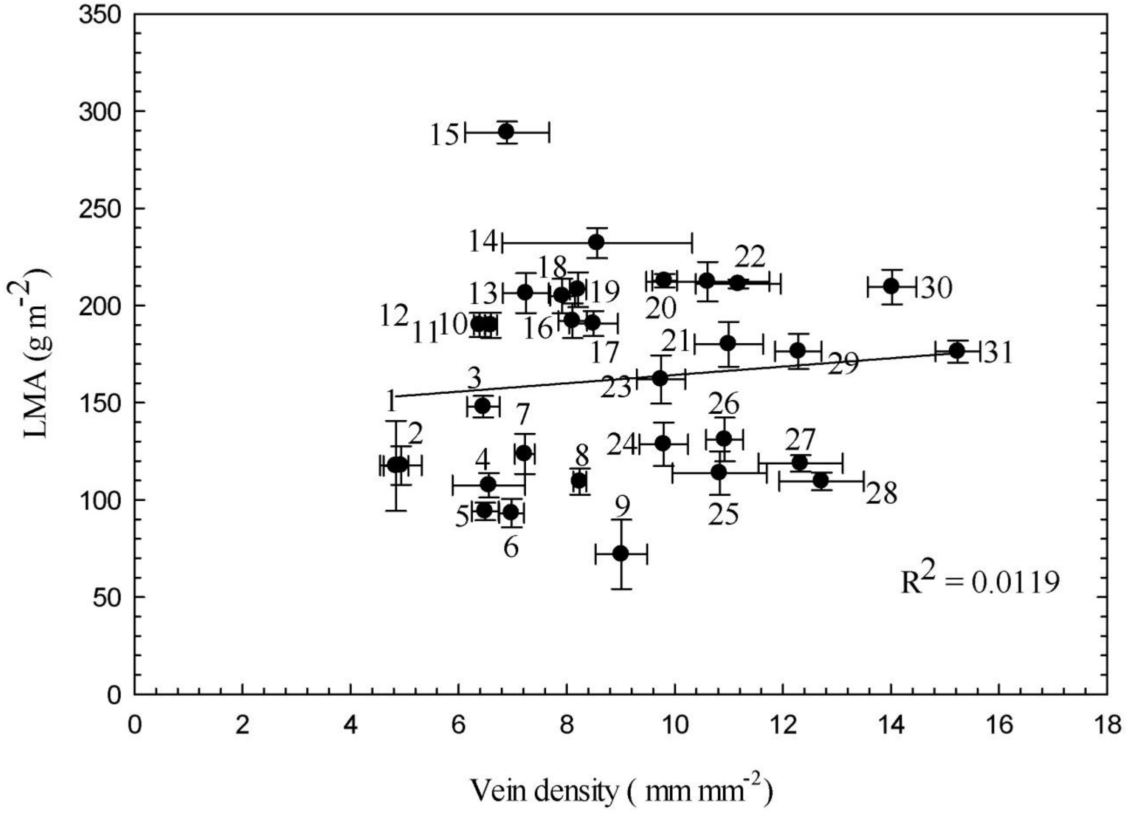


Figure 2.16. Correlation between g_{smax} (mmol H_2O m^{-2}s^{-1}) and vein density (mm mm^{-2}) in leaves of 13 common mangrove species; 1= *Aegiceras corniculatum*, 2= *Sonneratia alba*, 3= *Avicennia marina*4= *Aegialitis annulata*, 5= *Osbornia octodonta*, 6= *Bruguiera gymnorrhiza*, 7= *Rhizophora mucronata*, 8= *Rhizophora apiculata*, 9= *Rhizophora stylosa*, 10=*Xylocarpus australasicus*, 11= *Ceriops tagal*, 12= *Xylocarpus granatum*, 13= *Avicennia officinalis*. Symbols denote means with SES - standard error square for n = 10. A highly significant regression (y = 0.00568x + 8.095, R^2 = 0.79, $P < 0.001$) indicated a strong relationship between D_V (mm mm^{-2}) and g_{smax} (mmol H_2O m^{-2}s^{-1}).

Figure 2.17. Relationship between vein density and LMA of 31 species; 1 = *Cynometra ramiflora*, 2 = *Dolichandrone spathacea*, 3 = *Excoecaria agallocha*, 4 = *Scyphiphora hydrophyllacea*, 5 = *Xylocarpus rumphii*, 6 = *Xylocarpus granatum*, 7 = *Stemonurus apicalis*, 8 = *Xylocarpus australasicus*, 9 = *Avicennia alba*, 10 = *Myristica hollrungii*, 11 = *Heritiera littoralis*, 12 = *Luminitzera racemosa*, 13 = *Aegilitis annulata*, 14 = *Osbornia octodonta*, 15 = *Sonneratia alba*, 16 = *Nypa fruticans*, 17 = *Pemphis acidula*, 18 = *Acanthus ilicifolius*, 19 = *Aegiceras corniculatum*, 20 = *Avicennia marina*21 = *Avicennia officinalis*, 22 =*Bruguiera cylindrica*, 23 = *Bruguiera parviflora*, 24 = *Bruguiera sexangula*, 25 = *Rhizophora mucronata*, 26 = *Ceriops decandra*, 27 = *Ceriops tagal*, 28 = *Bruguiera exaristata*, 29 = *Bruguiera gymnorrhiza*, 30 = *Rhizophora apiculata*, 31 = *Rhizophora stylosa* Symbols denote means with SES – standard error square for n = 10. $R^2 = 0.01$, $P > 0.05$, indicated a lack of relationship between D_V (mm mm^{-2}) and LMA (g m^{-2}).



LMA (g m-2)
Vein density (mm mm-2)
0
50
100
150
200
250
300
350
0
2
4
6
8
10
12
14
16
18
R2 = 0.0119
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
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Figure 2.17.

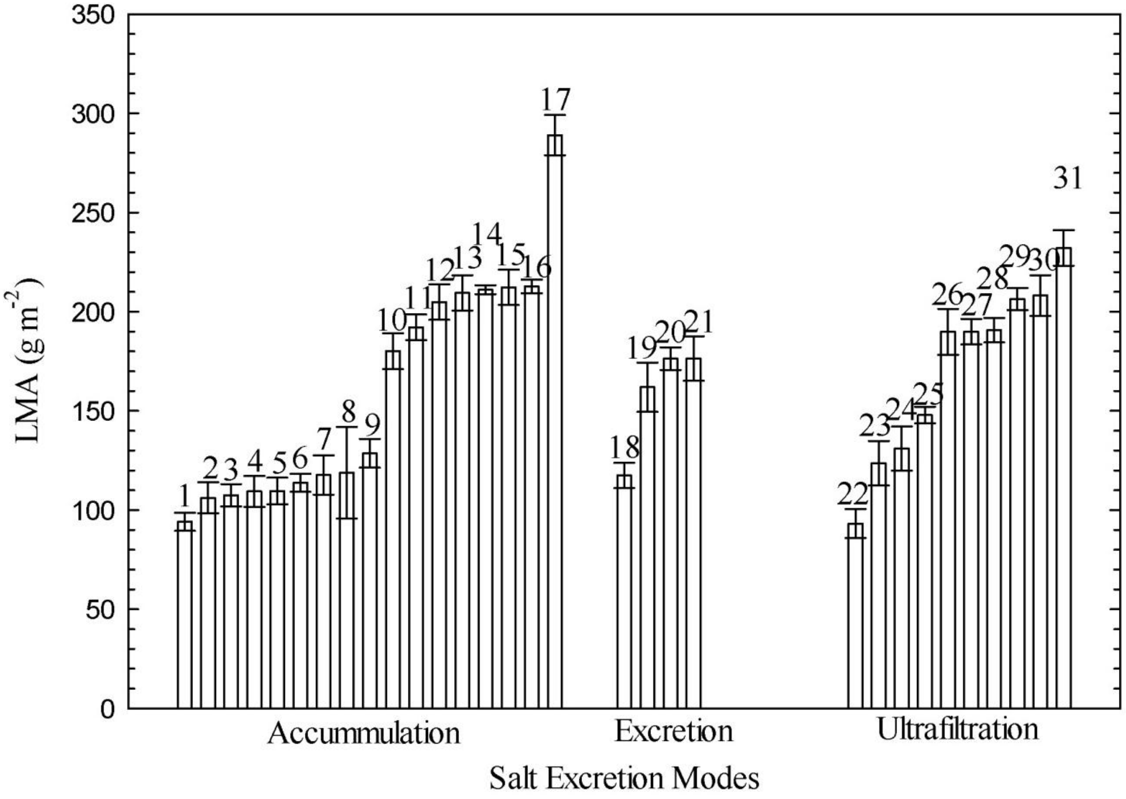

Figure 2.18. Variation in LMA with different salt excretion modes (SEM). Data points are means of sample size n = 10, with error bars denoting the standard deviation around the mean. Numbers 1 to 31 denote the respective species in appendix 2.1. LMA varied markedly among SEM. The salt accumulators ranged from 94.02±4.53 SD g m^{-2} in *Cynometra ramiflora* to 289.00±10.12 SD g m^{-2} in *Pemphis acidula*. The salt excretors ranged from 117.43±6.34 SD g m^{-2} in *Acanthus ilicifolius* to 176.23±5.67 SD g m^{-2} in *Avicennia officinalis*. The ultrafiltration species ranged from 93.14±7.32 SD g m^{-2} in *Bruguiera cylindrical* to 232.09±8.98 SD g m^{-2} in *Rhizophora stylosa*.

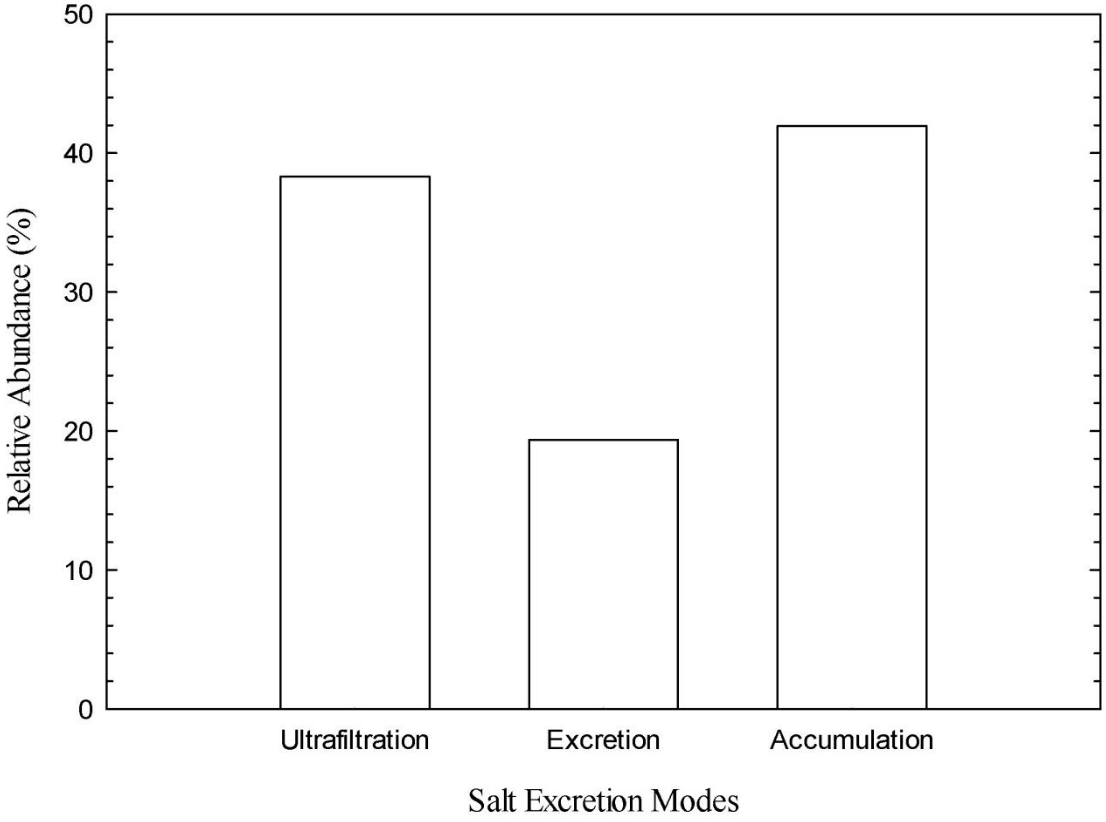

Figure 2.19. Percent relative abundance (%) of different salt secretion modes (SEM) across the 31 mangrove species. The three SEM, Ultrafiltration, Excretion, and Accumulation each comprised 38.71, 19.35, and 41.94 percent, respectively.

DISCUSSION

Plant functional traits represent plant adaptations to specific environments and resource-use strategy, and therefore provide valuable information for the analysis of community assembly (McGill *et al*. 2006, Ackerly and Cornwell 2007, Brodribb *et al.* 2007, Feild and Balun 2008, Poorter *et al*. 2009), ecosystem functioning and services (Diaz *et al*. 2007, Zhang and Cao 2009), and predicting evolutionary history of terrestrial plant diversity and determining fitness (Agarwal 2001; Brodribb and Feild 2010). The coexisting mangrove species exhibited marked differences in leaf traits (LMA, D_V) and photosynthetic gas exchange functional traits (A_{max}, g_{smax}) among different zones and growth forms. Photosynthetic gas exchange capacity was highest in species associated with MLT zone and decreased in the landward direction. D_V trait correlated positively with photosynthetic gas exchange traits (A_{max}, g_{smax}) and the LMA trait which is an excellent indicator of resource use strategy of a species was highest in species in MLT zone and decreased in the landward direction. Finally the differences in leaf functional traits reflect the prevailing biogeochemical environmental gradient.

Relationship between photosynthetic gas exchange, zonation, and plant growth forms

Previous studies have used photosynthetic gas exchange functional traits (A_{max}, g_{smax}) to assay productivity, growth and survival in mangrove ecosystem (Ball 1988, Passioura *et al.* 1992, Ball and Pidsley 1995, Clough *et al*. 1982, Clough 1998, Suwa *et al*. 2006, Suwa 211). For example; changes in net assimilation rate of two conspecifics, *Sonneratia alba* and *Sonneratia lanceolata,* significantly influence the growth and survival of the two species (Ball and Pidsley 1995). Low stomatal conductance in mangrove associated with salt balance is regulated by intracellular metabolism has been reported to limit growth (Passioura *et al*. 1992). Canopy structure in *Kandelia candel* had significant influence on photosynthetic photon flux density (Suwa 2011). Photosynthetic gas exchange capacity in *Rhizophora stylosa* differed significantly with canopy strata (Suwa and Hagihara 2008). A study on gas exchange capacity of two mangrove species (*Aegiceras corniculatum* and *Avicennia marina*) under glass house condition found low A_{max} and g_{smax} which in turn co-limited carbon assimilation rates, and therefore, generalized that mangroves have a narrow functional performance. The photosynthetic gas exchange information from the above studies are derived from one or two taxa from low diversity subtropical mangrove communities and therefore are limited for making reliable predictions on global mangrove productivity. More critical so, is the absence of comparable data from hyperdiverse mangrove communities such as those in New Guinea which has over 90% of the worlds' mangrove diversity (Giensen *et al*. 2007).

A current, widely held paradigm on functional diversity and performance of mangrove ecosystem *sensu* (Ball and Farquhar 1984a, Ball *et al*. 1988) is that mangroves are very conservative in their resource utilization and have high water use efficiency and, therefore, exhibit strong similarities in their functional performance. Stemming from the above widely held paradigm, my a priori hypothesis was that the hyper-diverse mangrove communities exhibit a narrow functional range despite their diverse phylogenetic affinities. In contrast to my hypothesis (high diversity mangrove communities in New Guinea exhibit a narrow photosynthetic gas exchange functional performance despite their wide phylogenetic affinities, I found that variation in the leaf functional performance of mangroves in diverse mangrove communities from variuos sites in New Guinea revealed significant variation in the photosynthetic gas exchange capacity of species across zonation and between growth forms. Rather, the results instead suggested that mangroves despite occupying narrow habitat range and pronounced morphological convergence have evolved functional and structural traits that enable variation in functional diversity and performance.

My results indicated that there are significant differences in A_{max} between different zones (Fig.2.6). This suggests that the differences in the A_{max} among different zones are influenced by the local biogeochemical environmental gradient (zonation). The duration of tides (mean low tide (MLT), medium high tide (MHT), and upper high tide (UHT), and Spring tide in the of back swamp mangrove (BSM) vary persistently throughout the year and the four different zones observed in my study reflect different tide durations. The longest tide duration was observed in the mean MLT and declined in the landward direction. Zones with the longest tide duration have the highest salinity exposure and vise-versa for zones with shortest salinity exposure. It is plausible; that the variation in A_{max} is a reflection of a gradient in the optimal physiological and functional performance range of individuals across biogeochemical environmental gradient, of which salinity appear to be the predominant factor. This speculation is supported by the PMC (pairwise multiple comparation of means) data which indicated significant mean differences between MLT and UHT zones. The PMC data (Table 2.3) indicated that the change in photosynthetic carbon assimilation rate changes gradually across the zonation. Mangrove species varied by two-fold in their photosynthetic carbon assimilation rate across all zones except UHT zone which varied by one-fold (Fig. 2.6, Table 2.4), ranging from 4.89 ± 0.23 SD µmol $CO_2m^{-2}s^{-1}$ in *Acanthus ilicifolius* to 19.02 ± 0.88 SD µmol $CO_2m^{-2}s^{-1}$ in *Avicennia marina*. Species also varied markedly within zones, with ~ one-fold, two-fold, three-fold differences in MLT, MHT, and UHT zones respectively. Differences in the photosynthetic carbon assimilation rate showed a continuum with species in the MLT exhibiting highest A_{max} (19.2 ± 0.88 SD µmol $CO_2m^{-2}s^{-1}$) with a mean of (16.22 ± 0.82 SD µmol $CO_2m^{-2}s^{-1}$) and decreased in the landward direction. The A_{max} between different growth forms varied significantly ($F_{2,10} = 4.69$, $P < 0.05$) (Fig. 2.7, Table 2.4), suggesting that different growth forms differ markedly in their light harvesting capacity. Large trees exhibited the highest A_{max} rate followed by small-medium trees then the shrubby species (Fig. 2.7, Table 2.4). Comparison across zonation showed highest g_{smax} (0.24 ± 0.03 SD mmol $m^{-2}s^{-1}$) in species inhabiting the MLT zone and decreased in the landward direction to a low of 0.097±0.001 SD mmol $m^{-2}s^{-1}$ in the UHT zone (Fig. 2.7). Matching of g_{smax} versus growth forms indicated highest g_{smax} rate

(0.24 ± 0.03 SD mmol $m^{-2}s^{-1}$) in a shrub (*Osbornia octodonta*) with a mean of 0.21 ± 0.0.016 SD, followed by large trees with a mean of 0.17 ± 0.02 SD mmol $m^{-2}s^{-1}$ and small-medium tree (0.099 ± 0.01 SD mmol $m^{-2}s^{-1}$) respectively (Fig. 2.7, Table 2.4).

Data on the relationship between photosynthetic functional traits (A_{max}, g_{smax}) and zonation suggested that the underlying soil substrate condition has significant influence on the gas exchange capacity of mangrove species. Species in the mean low tide (MLT), the most sun exposed zone, have the highest photosynthetic carbon assimilation rate. The highest photosynthetic carbon assimilation rate was observed in the MLT (most sun exposed) zoneand lowest in the BSM zone with the highest shade level. A similar trend was observed earlier (Ball and Farquhar 1984b, Ball *et al*. 1988); however, these studies reported consistently low A_{max} values (< 8.0 µmol $CO_2m^{-2}s^{-1}$) from a low diversity mangal system whereas my study based on New Guinea mangroves measured much higher high photosynthetic gas exchange capacities (mean A_{max} = 14.00 µmol $CO_2m^{-2}s^{-1}$ and mean g_{smax} = 0.17 mmol H_2O m^{-2} s^{-1} equaling those of fast growing terrestrial C_3 plants (Brodribb *et al*. 2007, Boyce *et al.* 2009, Brodribb and Feild 2010, Feild *et al*. 2011a, b). There are hints from previous studies on mangroves indicating higher A_{max} of 22.04 ± 1.02 µmol CO_2 $m^{-2}s^{-1}$ and g_{smax} of 0.27 ± 0.02 mmol H_2O $m^{-2}s^{-1}$ (Clough and Sim 1989), A_{max} of 11.9 ± 1.8 µmol CO_2 $m^{-2}s^{-1}$ (Sobrado *et al.* 1998), A_{max} of 17 µmol CO_2 $m^{-2}s^{-1}$ (Suwa and Hagihara 2008). These few studies were based on low sample sizes and under a controlled environment. Therefore, it is not possible to make direct inferences from these earlier studies to understand the factors responsible for the trends observed in this study. My data now provides better evidence that mangroves have a much wider functional performance than the long held view that mangroves are universally conservative plants (Ball and Farquhar 1984, Ball *et al*. 1988). For example, I observed an A_{max} range from 4.89 ± 0.23 µmol CO_2 $m^{-2}s^{-1}$ in *Acanthus ilicifolius* to 19.02 ± 0.88 µmol CO_2 $m^{-2}s^{-1}$ in *Avicennia marina* and a g_{smax} range of 0.1 ± 0.01 mmol H_2O $m^{-2}s^{-1}$ in *Bruguiera gymnorrhiza* to 0.24 ± 0.01 mmol H_2O $m^{-2}s^{-1}$ in *Sonneratia alba*.

Photosynthetic gas exchange rate varies markedly under different temperature, solar irradiance and hydroperiods (Krauss *et al*. 2006, Medina *et al*. 1989). Previous studies showed that A_{max} in mangroves in dry season reduced from 9.6 ± 2.0 to 4.7 ± 2.5 µmol $CO_2m^{-2}s^{-1}$ for plants in high salinity sites and from 11.9 ± 1.8 to 7.0 ± 1.5 µmol $CO_2m^{-2}s^{-1}$ for plants in low salinity sites (Sobrado 1999, Sobrado 2002). It is plausible that the variation in photosynthetic gas exchange capacities for the Motupore and Bootless Bay communities measured in this study are related to long dry season because I measured the photosynthetic gas exchange capacities during dry season (appendix 2.4). The effect of the dry season could have substantial influence because of lower rainfall or drier pervading air reduced maximal stomatal conductance. The data for Madang and Lae mangrove communities may not differ significantly throughout the year because of lack of pronounced seasonality.

The growth form (forest structure) and photosynthetic gas exchange data varied significantly between different growth forms but did not show any gradation with canopy height as previously reported by Saenger and Snedaker (1993). Saenger and Snedaker (1993) reported mangrove productivity (A_{max} and g_{smax}) is broadly correlated with forest height. The data in this study indicated that A_{max} and g_{smax} are not correlated with canopy height, but are rather correlated with the resource-use strategy of species as indicated by LMA data (Table 2.5). The trend observed in the relationship between photosynthetic assimilation and stomatal conductance rates are consistent with Cunningham *et al.* (1999), and Vendramini *et al.* (2001). These earlier studies showed that low LMA plants favor differential allocation to storage and defense versus high LMA plants with preferential allocation to photosynthesis and growth. A linear regression analysis of the A_{max} versus D_V (Fig. 2.15) and g_{smax} versus D_V (Fig. 2.16) showed highly significant correlations; $R^2 = 0.68$, $P < 0.001$ and $R^2 = 0.79$, $P < 0.001$ respectively, indicating a strong link between D_V and A_{max} and D_V and g_{smax}. This observation is consistent with those of Brodribb *et al*. (2007), Boyce *et al*. (2009, and Brodribb and Feild (2010). However, my results are the first to demonstrate that a relation between leaf venation anatomy and photosynthetic gas exchange capacity holds in plants that occur in a dry environment with a six month dry period of less than 50 mm rainfall (Appendix 2.20).

High photosynthetic gas exchange rates in some mangrove species have been correlated to rapid growth rates, which are typical of fast growing invasive species. For example, an exotic *Sonneratia apetala* that has a relatively high photosynthetic gas exchange rate (A_{max}, 12.0 ± 0.8 µmol $CO_2m^{-2}s^{-1}$ with a correspondingly fast growth rate has been successfully introduced into China for building a “green wall” along the coastlines (Chen *et al.* 2008). However, there are other invasive mangrove species that have relatively low photosynthetic gas exchange rates. For example, *Bruguiera sexangula* and *Rhizophora mangle* in Hawaii are introduced species but have low A_{max} of 5.3 ± 0.4 µmol $CO_2m^{-2}s^{-1}$ and 9.4 ± 1.2 µmol $CO_2m^{-2}s^{-1}$ respectively (Krauss and Allen

2003). I have measured a mean A_{max} of 10 µmol $CO_2m^{-2}s^{-1}$ and maximum of 19 µmol $CO_2m^{-2}s^{-1}$ in my study from the native mangrove species, i.e not invasive. My data implies that high rates of photosynthesis are not primarily associated with invasiveness characteristic of a species.

Relationship between leaf mass per area (LMA), zonation and growth form

Leaf mass per area (LMA, g m^{-2}) is a good correlate of leaf construction cost, which denotes the amount of resources invested in constructing the leaf and is often evaluated in terms of carbon and nutrients (Williams *et al*. 1987, 1989). Construction cost per leaf mass and LMA are positively correlated and vary with environmental and ecological characteristics of plants (Merino *et al*. 1982, Mooney and Gulmon 1982, Williams *et al*. 1987, 1989). Leaf construction costs per unit of mass, evaluated in carbon-based currency are highest in early successional and shortest-lived leaf longevity species and lowest in late secondary and longest-lived species (Grime 1979, Bazzaz and Picket 1980, Williams *et al*. 1989). LMA is also known to vary between different growth forms, for example, LMA in annuals is lower than chaparral shrubs (Miller and Stoner 1974, Chung and Barnes 1977), but in general LMA is highest under a high light, water, and nutrient environment and lowest at their opposite extremes (Mooney and Gulmon 1982). Construction cost per unit leaf area or LMA increases with daily photosynthetic photon flush density and is highest in open habitats with highest daily PFD and decreases with declining PFD. Low levels of daily photosynthetic carbon assimilation were also observed to be characteristic of lowest mass-based leaf costs and longest leaf duration (Williams *et al*. 1989, Poorter *et al*. 2009).

Investigation for trends in the LMA trait in a hyperdiverse mangrove community across zonation showed significant variation among different zones (Fig. 2.11, Table 2.5). The overall trend revealed in this study is that LMA varied consistently between the different ecological zones in the mangrove ecosystem (Fig. 2.11, Table 2.5). With the lowest mean LMA (129.37 ± 6.29 SD g m^{-2}) recorded in the BSM zone and the highest (209.51 ±7.88 SD g m^{-2}) recorded in the MLT zone (Fig. 2.11, Table 2.5). Plants in the MLT zone experience the highest level of physiological drought (high water constraints) and those in BSM zone have the lowest water use efficiency. Previous studies showed that LMA is positively correlated to mean solar radiance and leaf density which is a function of soil water availability, i.e. leaf density increases with increasing water limitation (Niinemets 2001, Poorter *et al.* 2009). My study showed highest LMA in the mean low tide zone (MLT, Fig. 2.11). Species in the MLT zone receive the maximum exposure to solar radiance, and experience the highest water constraint (Ball and Farquhar 1984, Ball *et al*. 1988, Passioura *et al*. 1992, Sobrado 2000, 2005) that potentially lead to higher leaf density. Therefore, the trend observed in my study is consistent with previous studies (Mooney and Gulmon 1982, Williams *et al*. 1989, Niinemets 2001, Poorter *et al*. 2009). These early studies found that LMA increases with increasing leaf density. Leaf density increases with increasing limitation in soil water availability (Williams *et al*. 1989, Castro-Díez *et al*. 2000, Niinemets 2001, Lamont *et al*. 2002, Poorter *et al.* 2009). Denser leaves correspond with greater proportion of sclerified tissues in lamina, small cells, lower water content and nitrogen content (Castro-Díez *et al*. 2000).

The relationship between LMA and growth forms indicated lowest mean LMA was measured in the large trees (129.3 ± 6.3 SD g m^{-2}) and the highest in the shrubby growth form (186.1 ± 8.1 SD g m^{-2}). My study found no significant mean difference between the growth forms. The trend in variation in LMA between different growth forms (Fig. 2.12) is congruent with previous studies (Miller and Stoner 1974, Chung and Barnes 1977, Niinemets 2001, Liu *et al.* 2010). The lack of relationship between LMA and growth form revealed from my study is consistent with many previous studies (Williams *et al*. 1989, Witkowski and Lamont 1991, Niinemets 2001). The above studies showed that LMA is correlated to leaf thickness, leaf density, mean solar radiance, and inversely related to precipitation, but not correlated to growth form. Another regional study investigating relationships between LMA, leaf anatomical traits and the climate variables of 558 broad-leaved and 39 needle-leaved shrubs and trees from 182 geographical locations covering all the earths major woody biomes showed no significant difference in LMA between growth forms, but rather LMA correlated positively with mean solar radiance, temperature, and negatively with precipitation (Niinemets 2001, Lamont *et al*. 2002). It can be deduced from these previous studies that the differences in LMA among the growth forms are indeed structural modification representing the underlying changes in leaf density. The variation in LMA is therefore linked to leaf density which is strongly connected to soil water availability and not necessarily plant structure or growth form (Castro-Díez *et al*. 2000, Niinemets 2001, Poorter and Bongers 2006). Other related studies showed that LMA and photon-flush density (PFD) are positively correlated, i.e. LMA is highest in leaves exposed to full sunlight and decreases with decreasing daily PFD (Merino *et al*. 1982, Mooney and Gulmon 1982, Williams *et al*. 1987, Williams *et al*. 1989). Studies on the worldwide leaf economic spectrum indicated that LMA is highest in the shrubby and tree growth forms with no marked differences between the two growth forms (Castro-Díez *et al.* 2000, Wright *et al*. 2005b; Liu *et al*. 2010)

Most mangroves at the leaf mass area level evolved xeromorphic structure, a strategy favoring nutrient conservation in nutrient poor soil environment (Small 1972, Janzen 1974, Chapin 1980, Chabot and Hicks 1982, Horner *et al.* 1988). For example, succulent and sclerophyllous species have different water use strategies; succulent and sclerophyllous species both have low LMA (g m^{-2}), but the former is accompanied by high leaf water content (LWC), while the latter is accompanied by low (LWC). In the former, high LWC does not directly reflect high content of photosynthetically active cytoplasm, since most of the water contained in the chlorenchyma is vacuolar water (Larcher 1995, Gibson 1996, Vendramini *et al*. 2001). LMA is also positively correlated to the resource-abundance level of an environment. For example, Low LMA species (sclerophyllous and succulent plants) were linked to resource-poor habitats (tender-leafed plants), and high LMA species were linked to a resource-rich habitat, which have preferential allocation to photosynthesis and growth (Cunningham *et al*. 1999, Vendramini *et al.* 2001, Suárez 2003). LMA across zonation and between growth forms showed no evidence of mangroves having a characteristic narrow functional performance range as claimed by Ball and Farquhar (1984) and Ball *et al.* (1988). There is instead a consistently significant difference across the full breath of mangrove zonation which failed to support my hypothesis.

The relationship between LMA and canopy structural characteristics without consideration of the interplay of other axes of leaf functional traits, in particular A_{max} and g_{smax} can be misleading. For example, a series of studies on the relationship between photosynthetic gas exchange and LMA trait showed a positive relationship (Merino *et al*. 1982, Mooney and Gulmon 1982, Williams *et al*. 1987, Williams *et al*. 1989). The shrubby growth form observed in this study having the highest LMA were located in the most sun-exposed zone, and large trees were in the least sun-exposed zone. Therefore, the LMA trend observed in this study could be explained in terms of degree of light exposure and not necessarily structural architecture.

Relationship between vein density (D_V) zonation and growth form

D_V of co-existing species varied significant among zones (Fig. 2.13, Table 2.4) and growth forms (Fig. 2.14, Table 2.4). D_V varied by ~ 100 % in all zones (Fig. 2.13, Table 2.3) and over 100 - 150 %in different growth forms with the exception of the small to medium trees (Fig. 2.14, Table 2.4). D_V traits are intimately linked to A_{max} and g_{smax} of a species (Brodribb *et al.* 2007, Boyce *et al*. 2009, Brodribb and Feild 2010). Indeed, a strong positive correlation was observed in A_{max} and D_V ($R^2 = 0.68$, $P < 0.001$, Fig.

2.15) and g_{smax} and D_V ($R^2 = 0.79$, $P < 0 .001$, Fig. 2.16). The trends observed in D_V versus zonation and D_V versus growth forms (Fig. 2.13, 2.14) indicated the co-existing species in different zones and growth forms differed markedly in their photosynthetic gas exchange capacity. My a priori hypothesis predicted no marked variation in functional performance of the diverse PNG mangrove ecosystem. The D_V observed across zonation and between growth forms did not support my hypothesis. The current observations further invalidate the widely held paradigm that mangroves are conservative and have a narrow functional range (Ball and Farquhuar 1984, Clough 1984, Ball *et al*. 1988, Brugnoli and Björkman 1992, Smith *et al*. 1991, Passioura *et al*. 1992, Sobrado 1999), which was also embraced in my hypothesis.

Relationship between vein density (D_V) and photosynthetic traits (A_{max}, g_{smax})

Vein density (D_V) was positively correlated to the photosynthetic traits (A_{max}, µmol $CO_2 m^{-2} s^{-1}$ and g_{smax}, mmol $m^{-2} s^{-1}$). The observed relationships (Fig. 2.15, 2.16) indicated a strong link between structural properties of the leaf vein system to the functional processes of water transport and photosynthetic performance of leaves. The data indicated that the photosynthetic capacity of leaves in mangroves is intimately linked to the vein density (D_V). The trends observed in this study conform to established work on D_V and photosynthetic gas exchange capacity, which revealed strong positive correlation between D_V and photosynthetic functional traits (A_{max}, $g_{smax;}$ Brodribb *et al*. 2007, Boyce *et al*. 2009, Brodribb and Feild 2010, Feild *et al.* 2011a, b). The D_V in mangrove leaves are almost equal to or greater than those of many tropical rainforest species (Brodribb *et al*. 2007, 2009,, Brodribb and Feild 2010, Feild *et al.* 2011a, b). However, recent evidence indicated leaf of tropical pioneer angiosperms possess an average vein density range from minimum of 13 mm mm^{-2} to maximum of 20 mm mm^{-2} (Feild *et al*. 2011a). This D_V range for tropical rainforest exceeds that of mangroves observed in my study (~ 5-15 mm mm^{-2}). However, there is an apparent strong overlap in the D_V of TRF and mangrove ecosystem. Increased D_V has been observed to parallel increased photosynthesis as a result of increase in proximity of irrigation network to the sites of photosynthetic apparatus (Brodribb *et al*. 2007, Brodribb and Feild 2010, Feild *et al*. 2011a).

Relationship between vein density and leaf mass per area

There was no observable relationship between LMA and D_V ($R^2 = 0.02$, $P > 0.05$) (Fig. 2.17). The lack of relationship between D_V and LMA could be a result of disproportionate intracellular volume dimensions associated with the succulent nature of mangrove leaves. For example, hydraulic proficiency is strongly correlated with vein architecture and distance between the distal ends of vein and transpiration site in leaves. Notably, minor vein branches that bypass the inefficient mesophyll space to linking directly with stomata (transpiration site) in leaves have increased hydraulic proficiency significantly, which subsequently increase A_{max} and g_{smax} (Brodribb *et al*. 2007). There is also a significant difference in the particle densities of salt secreting and non-salt secreting leaves. For example, intramembranous particle (IMP) densities and particle distributions in the plasma membrane and tonoplast (vacuole membrane) of the cells of salt-secreting and non-secreting leaves of *Avicennia germinans* showed that IMP densities of the protoplasmic and exoplasmic face of the plasma membrane and tonoplast were significantly higher in hypodermal cells of secreting leaves than of non-secreting leaves. Particle densities were higher in the plasma membrane and tonoplast of the mesophyll cells than the hypodermal cells. The protoplasmic face of hypodermal plasma membranes of secreting tissue has significantly high particle density (Balsamo and Thompson 1995). This study also observed disproportionate relative abundance between the three salt excretory modes (Fig. 2.19) Ultrafiltration (38.71%), Excretion (19.35%), and Accumulation (41.94%). Thus it is plausible that marked variation in the IMP densities between salt-secreting and non-secreting leaves coupled with the speculated disproportionate intracellular volume dimensions associated with succulent leaf structure may greatly increase the apoplastic volume of the leaf mesophyll with subsequent increases in path length of vein ending from mesophyll to transpiration site. This should therefore change the hydraulic properties by disproportionate enlargement of mesophyll dimension to vein-ending path length, thus obscuring any relationship in LMA and D_V. Thus, there is no evidence that having higher photosynthetic rates is traded-off with leaf durability in mangrove plants.

Relationship between leaf mass per area and salt-excretion modes

Examination of the leaf mass area of the co-existing species showed significant difference among the different salt excretion modes (Fig. 2.18, Fig. 2.19). Because F-test was significant a pairwise multiple comparison (PMC) procedure (Holm-Sidak method) was used to explore the nature of these SEM (salt excretion modes), namely; ultrafilters, accumulators, and salt excretors differences. The PCM test showed significant difference between ultrafilters and accumulators as well as between excretors and accumulators, but no difference between ultrafilters and excretors. Salt-accumulating species exhibited the highest LMA (289.00 ± 10.12 SD g m^{-2}), followed by ultrafiltratring species (232.09 ± 8.98 SD g m^{-2}) and salt-excreting species (176.23±5.67 SD g m^{-2}). The LMA, as described above, correlates positively with carbon assimilation and growth (Merino *et al*. 1982, Mooney and Gulmon 1982, Williams *et al*. 1987, Williams *et al*. 1989, Niinemets 2001). Species with low LMA are known to be associated with resource-poor environment, low assimilation rate, and slow growth rate, while the reverse is true for high LMA species (Grime 1979, Bazzaz and Picket 1980, Williams *et al*. 1987, Williams *et al*. 1989). LMA has been shown reflect the leaf thickness and density traits, and has been shown to correlate with photosynthetic capacity per unit area (Niinemets 2001). Niinemets (2001) showed that greater leaf thickness is associated with greater leaf photosynthetic rate per unit area because of accumulation of photosynthetic compounds. The higher LMA observed in species associated with most exposed (MLT) zone in my study conform to this explanation by Niinemets (2001). Interestingly, the observed trend implies that species in different salt-excretory modes have different resource-use strategies. For example, salt accumulators and ultrafilters with their characteristic high LMA imply that these species are investing in rapid growth while opposite may be the case for the salt secretors. This marked variation in resource strategy between co-existing species from different salt-excretion modes suggested that co-existing mangrove species inhibiting a narrow habitat range have diverse functional performance.

The data from the leaf level functional traits (A_{max}, g_{smax}, D_V, LMA, and SEM) from mangal systems in New Guinea revealed significant differences in functional performance within their relatively narrow habitat range. The data suggest that mangroves have high photosynthetic gas exchange capacity and subsequently high net primary productivity. In addition, I found that water loss rates of mangroves were relatively high to meet high hydraulic demands of high CO_2 uptake. The data from my study are not congruent with my a priori hypothesis. The distinct variation and gradation in the functional performance of species established in my study invalidates the long held paradigm of mangroves being highly conservative (i.e. high water use efficiency hence low assimilation rate; Ball and Farquhar 1984, Ball *et al.* 1988).

Implications for management of mangrove ecosystems

My research demonstrates that mangroves varied markedly in their functional performance despite their inhibiting narrow habitat range. My results suggest that the ecological success of mangrove ecosystem as one of the carbon rich tropical forest is intertwined in the physiological and functional traits of its constituent plant species. Detailed understanding of the full breadth of ecophysiological and functional performance of species is a requisite to sustainability of mangrove ecosystems. It is no longer acceptable to view mangroves as conforming to a single functional stereotype. Instead, I have found evidence for both resource profligate as well as resource conservative mangrove species. A focus on the high species diversity mangrove forests in New Guinea has allowed for the detection of these diverse co-existing functional types in the mangrove biome for the first time.

Plant functional traits represent plant adaptations to specific environments and resource-use strategy, and therefore provide valuable information for the analysis of community characteristics. Evolution of high diversity in mangrove communities is linked to the functional characteristics of species; hence, detailed understanding of the physiological and functional characteristic of the community is prerequisite to sustainable management of mangrove ecosystems.

A broader analysis of my findings from this chapter will be integrated with wood anatomical and hydraulic functional traits in chapter four.

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APPENDICES

Appendix 2.1: Species list of the 31 New Guinea mangrove species with their corresponding salt excretion modes and rooting sytem types.

Species	**ID Code**	**Salt Excretion Modes**	**Root type**	**LMA**	**SD**
Cynometra ramiflora	1	Accumulation	Plank buttress	94.019	4.530
Dolichandrone spathacea	2	Accumulation	No modified Roots	106.128	7.800
Excoecaria agallocha	3	Accumulation	No modified Roots	107.450	5.600
Scyphiphora hydrophyllacea	4	Accumulation	No modified Roots	109.321	7.810
Xylocarpus rumphii	5	Accumulation	Plank buttress	109.507	6.700
Xylocarpus granatum	6	Accumulation	Plank buttress	113.731	4.560
Stemonurus apicalis	7	Accumulation	Stilt Root	117.667	9.890
Xylocarpus australasicus	8	Accumulation	Plank buttress	118.756	23.120
Avicennia alba	9	Accumulation	Pneumatophores	128.593	7.231
Myristica hollrungii	10	Accumulation	Stilt Root	180.006	9.020
Heritiera littoralis	11	Accumulation	Plank buttress	192.100	6.430
Luminitzera racemosa	12	Accumulation	Pneumatophores	204.810	8.990
Aegilitis annulata	13	Accumulation	No modified Roots	209.413	8.900

Cont…/

Species	**ID Code**	**Salt Excretion Modes**	**Root type**	**LMA**	**SD**
Osbornia octodonta	14	Accumulation	No modified Roots	211.026	2.300
Sonneratia alba	15	Accumulation	Pneumatophores	212.218	8.900
Nypa fruticans	16	Accumulation	No modified Roots	212.678	3.424
Pemphis acidula	17	Accumulation	No modified Roots	289.000	10.120
Acanthus ilicifolius	18	Excretion	No modified Roots	117.434	6.340
Aegiceras corniculatum	19	Excretion	No modified Roots	161.914	12.450
Avicennia marina	20	Excretion	Pneumatophores	176.234	5.671
Avicennia officinalis	21	Excretion	Pneumatophores	176.353	11.230
Bruguiera cylindrica	22	Ultrafiltration	Knee-like	93.140	7.320
Bruguiera parviflora	23	Ultrafiltration	Knee-like	123.554	11.200
Bruguiera sexangula	24	Ultrafiltration	Knee-like	130.987	11.110
Rhizophora mucronata	25	Ultrafiltration	Stilt Root	147.863	4.210
Ceriops decandra	26	Ultrafiltration	Knee-like	189.833	11.560
Ceriops tagal	27	Ultrafiltration	Knee-like	189.938	6.450
Bruguiera exaristata	28	Ultrafiltration	Knee-like	190.689	6.200
Bruguiera gymnorrhiza	29	Ultrafiltration	Knee-like	206.292	5.560
Rhizophora apiculata	30	Ultrafiltration	Stilt Root	208.120	10.230
Rhizophora stylosa	31	Ultrafiltration	Stilt Root	232.087	8.980

Appendix 2.2. Rainfall chart for the six study sites.

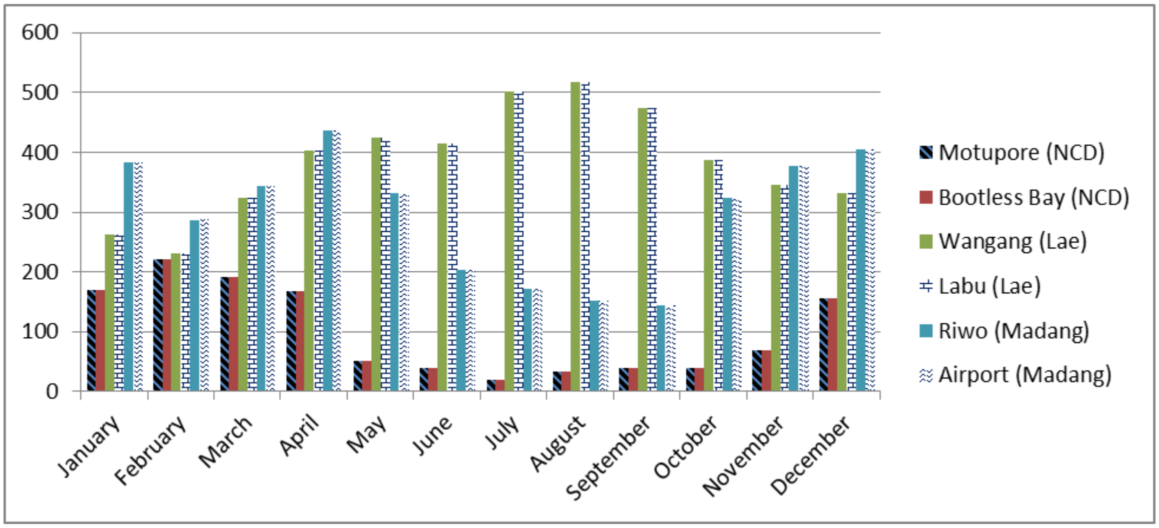

Figure 20.0. Mean monthly rainfall distribution from 33 years record for the six study sites (McAlpine *et al.* 1983).

Appendix 2.3. Species checklist of the 31 mangrove species, comprising 20 genera and 17 families from New Guinea investigated in this study.

Family	**Scientific Names (Species)**	**Common Name(s)**
Acanthaceae	*Acanthus ilicifolius* L.	Holly mangrove
Acanthaceae	*Avicennia alba* Blume	
Acanthaceae	*Avicennia marina* (Forssk.) Vierh.	White mangrove, Grey Mangrove
Acanthaceae	*Avicennia officinalis* L.	
Arecaceae	*Nypa fruticans* Wurmb.	Mangrove palm
Bignoniaceae	*Dolichandrone spathacea* (Lf.) K. Sch.	
Caesalpinaceae	*Cynometra ramiflora* L.	
Combretaceae	*Luminitzera racemosa* Willd.	Black mangrove
Euphorbiaceae	*Excoecaria agallocha* L.	Blind-Your-Eye Mangrove
Icacinaceae	*Stemonurus apicalis* (Thwaites) Miers	
Lythraceae	*Pemphis acidula* J.R.Forst & G.Forst	
Meliaceae	*Xylocarpus australasicus* Ridl.	Cannonball Mangrove
Meliaceae	*Xylocarpus granatum* Koen.	Cannonball Mangrove
Meliaceae	*Xylocarpus rumphii* (Kostel.) Mabb.	Cannonball Mangrove
Myristicaceae	*Myristica hollrungii* Warb.	
Myrsinaceae	*Aegiceras corniculatum* (L.) Blanco	River Mangrove
Myrtaceae	*Osbornia octodonta* F. Muell.	Myrtle Mangrove
Plumbaginaceae	*Aegilitis annulata* R. Br.	Club Mangrove
Rhizophoraceae	*Bruguiera cylindrica* (L.) Blume	
Rhizophoraceae	*Bruguiera exaristata* Ding Hou	
Rhizophoraceae	*Bruguiera gymnorrhiza* (L.) Lam	Large-leafed Orange Mangrove
Rhizophoraceae	*Bruguiera parviflora* (Roxb.) Wight & Arn. Ex Griff.	Small-leafed Orange Mangrove
Rhizophoraceae	*Bruguiera sexangula* (Lour.) Poir.	Upriver Orange Mangrove
Rhizophoraceae	Ceriops decandra (Griff.) Ding Hou	Yellow mangrove
Rhizophoraceae	Ceriops tagal (Perr.) C.B. Rob.	Yellow mangrove

Cont…/

Family	**Scientific Names (Species)**	**Common Name(s)**
Rhizophoraceae	*Rhizophora apiculata* Blume	Tall-stilted Mangrove
Rhizophoraceae	*Rhizophora mucronata* Lam.	
Rhizophoraceae	*Rhizophora stylosa* Griff.	Red Mangrove
Rubiaceae	*Scyphiphora hydrophyllacea* F. C. Gaertn.	
Sonneratiaceae	*Sonneratia alba* Sm.	Mangrove Apple
Sterculiaceae	*Heritiera littoralis* Ait.	Looking-glass Mangrove

CHAPTER III: WOOD MECHANICAL-HYDRAULIC FUNCTION ACROSS 31 SPECIES OF NEW GUINEA MANGROVES

ABSTRACT

Wood traits are an important source of information about how trees are coping with conflicting requirements of optimal hydraulic conductivity and safety. In this study, I investigated the variation in wood and hydraulic functional traits of 31 mangrove species across zonations and among different growth forms from six hyperdiverse mangrove communities in New Guinea. The study tested the hypothesis that the hyperdiverse mangrove communities in New Guinea exhibit a narrow functional performance despite their wide phylogenetic affinities.

Wood anatomical traits (wood density, vessel diameter, vessel density, hydraulic mean vessel diameter) of 31 co-existing mangrove species in six hyperdiverse mangrove communities in New Guinea varied markedly across different zonation bands. Wood density (P_{wood}) varied significantly among different zones ($F_{3,21} = 40.96$, $P < 0.0001$). P_{wood} varied by over 30% among different growth forms, but the differences were not significant ($P > 0.05$). Maximum P_{wood} (0.94 ± 0.03 g m-3) was observed in the mean low tide (MLT) zone and decreased in the landward direction. P_{wood} varied significantly among different rooting system types ($F_{4,27} = 6.33$, $P < 0.001$).

Vessel density (V_d) varied significantly among different zones ($F_{3,16} = 5.01$, $P < 0.01$) but variation was not significant among different growth forms ($F_{2,15} = 1.66$, $P > 0.22$). Vessel diameter (d_V) varied significantly among different growth forms ($F_{2,15} = 4.57$, $P < 0.03$) but did not significantly differ among the zones ($F_{2,17} = 0.33$, $P > 0.72$).

A linear correlation of P_{wood} and leaf mass area showed no significant correlation ($r^2 = 0.10$, $P > 0.08$). A linear correlation of vessel density and vessel diameter showed an inverse relationship ($r^2 = 0.18$, $P < 0.02$). Vessel density was also inversely correlated to weighted hydraulic mean diameter ($r^2 = 0.22$, $P < 0.01$).

A linear correlation of potential hydraulic conductivity (K_P) and vein density showed no significant correlation ($r^2 = 0.0005$, $P > 0.05$). K_P was inversely correlated to: V_d ($r^2 = 0.21$, $P < 0.01$), strongly correlated to d_V ($r^2 = 0.95$, $P < 0.0001$), and strongly correlated to d_h (mean hydraulic diameter, µm) ($r^2 = 0.78$, $P < 0.0001$).

A linear correlation of calculated leaf area specific hydraulic conductivity (K_L) and vein density showed a significant relationship ($r^2 = 0.47$, $P < 0.05$). K_L was correlated to A_{max} ($r^2 = 0.56$, $P < 0.05$).

INTRODUCTION

Mangroves are tropical and subtropical forests occupying the inter-tidal zones along coastal shorelines and river deltas. Mangroves support an array of global and biogeochemical functions, including providing fisheries (Baran and Hambrey 1998, Barbier 2000, Kairo *et al*. 2001), facilitating production of organic matter, hydrological and biogeochemical cycles (Briggs 1977, Clough and Attiwill 1975, Malhi and Grace 2000, Bouillon *et al*. 2008a,b, Donato *et al*. 2011), offering shoreline protection, providing sediment accretion through trapping and accumulating silts, retarding the erosive impact of tidal waves, tsunami, storm and cyclone surges, filtering suspended particulate matter and debris from terrestrial runoff and floods, and maintaining the carbon balance of tropical coastal ecosystems (Field 1995, Dittmar *et al*. 2006, Vermaat and Thampanya 2006, Bouillon *et al.* 2008b, Das and Vincent 2009). Mangroves also provide substantial subsistence products for coastal communities, including fuel wood, construction wood, food, and traditional medicines (Bandaranayake 2002).

The constituent species of mangrove communities exhibit convergences in their overall functional and morphological characteristics (Lugo and Snedekar 1974, Tomlinson 1986). For example, mangroves have evolved similar functional, ecological, and morphological characteristics, such as aerial roots, thick succulent leaves, glossy color, leaf position angled > 90^o and viviparous reproduction (Tomlinson 1986). Mangrove communities often display spatial zonation based on the gradation in the biophysical and geochemical environment with species' specialization (MacNae 1968, McKee 1993, Bunt 1996, Matthijs *et al*. 1999, Hopper-Speer 2011). Mangrove species are rarely found outside intertidal areas, and mostly occur between mean sea level and the level of mean high water spring tides (Lear and Turner 1977, Belperio 1979). Mangroves species share similar light climate requirements with their closes tropical rainforest species. Example, *Carallia bractiata* (Rhizophoraceae) and *Duabanga mollucana* (Lythraceae) are light demanders like their close mangroves affinities (*Rhizophora* spp) and *Pemphis acidula* respectively (Percival and Womersley 1975, Tomlinson 1986).

Serving as a carbon sink, mangroves store ~ 1.023 x 10^6 kg C $ha^{-1}yr^{-1}$ with 49-98% stored in the organic soil (Danato *et al*. 2011). This in contrast to 9.0 x 104 kg C $ha^{-1}yr^{-1}$ above ground in Southeast Asia tropical rain forest (Iverson *et al*. 1993) and 1.5 x 104 kg C $ha^{-1}yr^{-1}$ above ground in Amazon rain forest (Mahli and Grace 2000) is remarkably high. Mangroves also exert a strong influence on coastal geomorphology, making a unique contribution to carbon biogeochemistry in coastal seawater (Twilley *et al*. 1992) and play an important role in the oceanic carbon cycle (mineralization, burial of organic carbon, carbonate production and accumulation that take place in the coastal ocean; Gattuso *et al*. 1998, Mackenzie *et al*. 2004, Duarte *et al*. 2005), and in intertidal sedimentology.

Wood traits are emerging as core plant functional traits because of their importance in safety, hydraulics, carbon storage, architecture, defense, and growth (Meinzer *et al*. 2001, 2003, Santiago *et al.* 2004, Jacobsen *et al.* 2008, Chave *et al*. 2009, Robert *et al.* 2009, Poorter *et al*. 2010). There is some emerging evidence that wood traits are better predictors of whole plant ecophysiological strategy and performance because they reflect longer term investment-resource-use strategies of plants as compared to leaves that are shorted lived (Poorter *et al*. 2010, Baraloto *et al*. 2010). Wood traits (wood density, vessel density, vessel diameter) and stem hydraulic traits (specific potential hydraulic conductance, specific leaf area conductivity, Huber value) are important information sources regarding how trees manage their conflicting demands for optimal hydraulic conductivity, safety (Kobe *et al*. 1995, Poorter and Bongers 2006, Robert *et al*. 2009, Poorter *et al*. 2010), and their subsequent influence on photosynthesis, productivity, growth, and survival (Brodribb *et al*. 2007, Feild and Balun 2007, Hudson *et al*. 2010). Wood hydraulic traits have been shown to have an intimate relationship with photosynthetic gas exchange, productivity, and growth rates (Brodribb and Feild 2000, Brodribb *et al*. 2007, Brodribb and Feild 2010). Variation in gas exchange capacity across different growth forms has been related to hydraulic constraints of the vascular tissue (Meinzer *et al*. 1999, 2003, Brodribb and Feild 2000). In woody plant species, growth and survival rates are correlated to wood traits. For example, a study on wood traits of 42 rainforest tree species showed wood density (P_{wood}) was positively correlated with survival rate and negatively correlated with growth rate (Poorter *et al*. 2010). Wood allocation in vessel number versus size was suggested to be an investment in hydraulic safety versus hydraulic conductivity (Robert *et al*. 2009, Poorter *et al*. 2010). Allocation in parenchyma tissue versus fibres was regarded as an investment in storage versus mechanical strength (Poorter *et al.* 2010). Wood functional traits, vessel diameter (V_d), and specific potential hydraulic conductance (K_P) are positively correlated to growth rate (Poorter *et al.* 2010). Moreover, wood traits have recently gained prominence as functional traits due to their contribution to mechanical stability, defense, carbon storage, growth, and survival (Santiago *et al.*2004, Jacobsen *et al.* 2008, Chave *et al.* 2009, Zhang and Sao 2009, Poorter *et al.* 2010).

Wood density (P_{wood}) measured as gram per cubic meter (g m^{-3}) is an important trait to the architecture of a plant, and an important determinant of performance (height growth, light capture, and mechanical stability) of a tree (Aiba and Nakashizuka 2009). Wood density has been linked to growth-survival trade-off observed in woody plants (Kitajima 1994, Kobe *et al*. 1995, Santiago *et al.* 2004; Poorter and Bongers 2006, Poorter *et al*. 2010). For example, low wood density is associated with fast growth because of cheap volumetric construction costs of the wood (Putz *et al*. 1983, Hacke *et al*. 2001, Sterk *et al*. 2006, Poorter *et al*. 2010). High wood density is correlated with high survival because of biomechanical and hydraulic safety (Putz *et al*. 1983, Hacke *et al*. 2001, Sterk *et al*, 2006) and higher resistance against herbivores, pathogens, and potential damage by falling woody debris (Augspurger and Kelly 1984, Van Gelder *et al*.

2006, McCarthy-Neumann and Kobe 2008). Mechanical properties of wood have also been studied through comparison of different species and are well-described by wood density and growth forms (Köhler 2000, Köhler *et al*. 2000).

Although it has been long recognized that wood density and xylem traits are key determinants of plant performance, there are very few studies that have investigated the relationship between wood anatomy and hydraulic functional traits in mangroves (Sobrado 2006, Fonti *et al*. 2010). In addition, the relationship between wood functional traits and zonational distribution of mangroves remains poorly understood (Schmitz *et al.* 2006, Robert *et al.* 2009). Previous studies are mostly based on low number of mangrove taxa (usually one to two species from low diversity mangrove communities). Wood traits in mesophytes (land plants) influence leaf photosynthetic traits and subsequently linked to primary production (Brodribb *et al.* 2007, Boyce *et al*. 2009, Brodribb and Feild 2010). However, there is no study so far for mangrove species that links leaf and wood functional traits together to understand the diversity of mangrove ecophysiological performances. Here I examined leaf and stem hydraulic functional traits in 31 species of mangroves to understand the functional relationships between these traits and how they might be associated with the distribution of species in hyperdiverse mangrove communities. The co-existence of high number of species in mangrove communities in New Guinea could represent the diversity of evolutionary functional strategies that underlie the evolution of species rich mangrove communities. Thus, wide variation in functional traits and their subsequent differential influences on productivity, growth rates, survival, and associated trade-offs could provide a possible explanation for the [co-existence of high species' within a single zone in the New Guinea mangroves.

There are very limited data on the wood functional traits of mangroves (Menezes *et al*. 2003, Verheyden *et al*. 2004, 2005, Schmitz *et al*. 2006). These studies investigated presence of annual growth rings (Menezes *et al*. 2003, Verheyden *et al*. 2004) and the relationship between vessel density, number of vessels per mm^2 (V_d), and salinity gradient (Schmitz *et al*. 2006). The annual growth ring data indicated that there is temporal variation in vessel density (V_d), with high V_d associated with dry conditions and low V_d associated with high precipitation (Menezes *et al*. 2003, Verheyden *et al*. 2004). There was a positive correlation between V_d and salinity gradient (Schmitz *et al.* 2006).

Mangroves exhibit definable zonation bands within the intertidal zone and reflect differential resource-use stratigies and trade-offs in response to prevailing biogeochemical environmental gradient. Therefore, information on how each species adapt to the zonation band is critical to understanding the functional performance of the species that enables co-existence of high diversity in a narrow ecological range. Yet, there is no information on the relationship between zonation and the wood characteristics of species that successfully occupy these distinct biogeochemical bands. Within the zonation bands, different growth forms may be persistent, example; in MLT zones shrub and small-medium size trees are common and large trees are absent. Mangroves have evolved differential rooting system types (RST) that appear to be coordinated with tidal activities. Different zonation bands appear to have characteristic ecological rooting structures. For example, prop or stilt roots are most abundant in highly unstable environments or mean low tide zone (MLT), knee-like rooting ecology predominate in the medium high tide (MHT) zone, and buttresses are predominant in the upper high tide zone (UHT). The pneumatophore RST seems to predominate in the between MLT and

MHT zones. It is plausible that the ecology of these different RSTs is partly shaped by the wood property of the whole plant. Understanding the relationship between the different RSTs and zonation may better our understanding on the variation in the functional performance of mangroves. However, this is a gap in our understanding of the relationship among different RSTs and zonation bands. My study will for the first time attempt to understand the relationship between RSTs and zonation, wood density and zonation, growth form and wood density. I will for the first to investigate variation in wood functional traits among three different growth forms, four different zones and five root system types.

I hypothesis that wood functional traits (P_{wood}, vessel diameter (d_V), vessel density (V_d), K_P, K_S, K_L, H_V) in the hyperdiverse co-existing mangrove communities in PNG should exhibit a narrow functional range despite their wide phylogenetic affinities. My hypothesis embraces the current widely held view on mangrove physiological and functional ecology that a stressful environment has evolutionarily boxed in the range of mangrove ecophysiological possibilities (Ball and Farquhar 1984, Ball 1988, Ball *et al*. 1988). It has been postulated that mangroves function as highly conservative plants in terms of water use and photosynthetic capacity (Ball and Farquhar 1984, Sobrado 1999). To test this hypothesis, I provide the first investigation on the variation in the wood functional traits (P_{wood}, Vessel diameter, Vessel density, K_P, K_S, K_L, H_V) across zonation gradients and growth habit in diverse New Guinea mangrove taxa. I also examined how these traits are linked to the leaf functional traits (D_V, LMA, A_{max}, g_{smax}). These results from my research will fill in a long-standing gap in our understanding of the functional performance of mangroves from hyperdiverse mangrove communities.

MATERIALS AND METHODS

Field sites and plant species

Location and climate

The study was conducted in six tropical mangrove communities in PNG, namely: the Motupore Island mangrove (09^{o}31’S, 147^{o}17’5E), and Bootless Bay mangrove (09^{o}30’S, 147^{o}16’E) within Central province, the Labu mangrove (06^{o}45’S, 146^{o}57’E), and Wangang mangrove (06^{o}44’S, 147^{o}01’E) within Morobe province, and the Riwo (05^{o}08’S, 145^{o}47’E), and Madang airport mangrove (05^{o}12’S, 145^{o}47) within Madang province (Fig. 2.0). The physical, climate (Table 2.1), and biogeochemical environment of the six study sites are described in Chapter Two.

Wood traits investigation

I sampled 10 to 15 mature undamaged stem segments ranging in size (~3-10 cm length x ~1-2 cm diameter) of 30 (excluding *Nypa*) New Guinean mangrove species from which a photosynthetic gas exchange study (my project one) was carried out. From the initial 31 species sampled for photosynthetic gas exchange study, *Nypa fruticans* (monospecific mangrove palm) was omitted because of difficulty in obtaining its wood. The stem segments of the 30 mangrove species were excised with secateurs, stored in Ziploc bags, and transported to a field laboratory for wood trait assessment.

Because the stem xylem hydraulic properties are sensitive to light environment, I ensured that branches were collected from a uniform light environment (Feild *et al*. 2002). Specifically, all wood samples were taken from branches that were exposed to 100% open sky. An assumption of this method is that field observation of light environment reflects the light environment that stem development occurred in. In the case of mangroves, which are short in stature and the forests are characterized by a low leaf area index (Méndez-Alonzo *et al.* 2008), this assumption is likely non-problematic. Wood traits; wood density (P_{wood}); potential sapwood area hydraulic conductivity (K_P); Huber value (H_V); specific-leaf area conductivity (K_L); vessel density (V_d); and vessel diameter (d_V) were measured from stem segments from which leaf functional traits measured as described in turn. I undertook this approach to enable comparison of leaf and wood functional traits.

Xylem anatomy

Xylem anatomy was measured in the field laboratory from transverse sections of stem segments that were recut and manually (free hand) sliced into five thin slices (~0.1 mm thick) with a fresh razor blade. The sapwood cross-sectional area (SA) of a representative area of stem tissue was determined just below the supported leaf area for each stem segment. I then stained the sections (slices) in 1% aqueous toluidine blue in a Petri dish for ~ 5 minutes. Stained sections were then removed, rinsed with water to remove excess stain, and mounted on microscope slides in glycerol and imaged under 100x magnification. Photographs were taken with a camera (Nikon, Japan) attached to a microscope (Olympus CH-2 w/Trinocular Head, USA). SA for each species was calculated from the mean of the five cross-sections minus their pith area (Sperry *et al.* 1988, Feild *et al.* 2001, Hudson *et al.* 2010) using ImageJ software (National Institute of Health, Bethesda, Maryland, USA). Vessel density (V_d, number of vessels per mm^{-2} of stem surface area) was measured for each stem. V_d was estimated by measuring number of vessels in one millimetre square area (1 mm^2). The vessel diameter (d_V, µm) for each species was derived from transverse sections from five stem segments of each species imaged from a microscope at 200x. To quantify d_V, I measured the lumen of each element in a stem cross section by tracing, using ImageJ to determine the area of the vessel lumen. I then used the diameter of a circle with equal area to calculate the mean d_V (µm) of 10 vessels for the species (Hudson *et al*. 2010). Vessel density (V_d, number of vessels mm^{-2}), for each species was estimated from the same images in which d_V was determined.

Wood density

For wood density (P_{wood}) measurement, 3 x (~6-10 cm length) segments of the branches and stems from the 30 sampled species were cut and placed in Ziploc plastic bags and transported to the field laboratory. The stem segments were then recut in the laboratory into ~2-3 cm length segments and debarked. The debarked segments were then split in the center and the pith tissue scrapped off with a stainless steel, sharp pointed screwdriver. I then pinned the split pieces one by one using a syringe and needle and recorded the weight of the fresh stem by inserting the split segments inside a beaker of water on an electronic balance. The displacement weight, which is equivalent in volume to the segment (= cm^3), was then recorded for 10 segments of each species. Stems segments were then labeled and placed inside a small brown envelope; oven dried for 48 hours at 60-70^oC; and measured the dry weight. The P_{wood} was then calculated using the following equation: P_{wood} = Dry weight (DW, g)/Volume (cm^3) (Aiba and Nakashizuka 2009, Hudson *et al*. 2010, Poorter *et al*. 2010).

Hydraulic traits measurements

Potential stem hydraulic conductivity

The potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}$ MPa^{-1}) expresses rate at which a unit mass of water is transported through a unit xylem sapwood area per unit pressure gradient. It estimates the hydraulic conductivity of a given stem using Hagen-Poiseuille law (Equation 1), which incorporates the vessel density (V_d) and mean hydraulic diameter (d_h; Equation 2) traits. K_P is a proxy of K_S (true measure of hydraulic efficiency of xylem sapwood area in conducting water). K_P is usually higher than K_S because it does not take into consideration the different resistance in the vessel conduits, such as vessel end wall (perforation plates) and pit apertures. To determine this theoretical hydraulic limit, the sum of all vessel diameters to the fourth power (Σd_V^4) was used to predict hydraulic conductance according to the Hagen-Poiseuille Law (Sperry and Saliendra 1994, Choat *et al*. 2005). The hydraulic diameter (d_h) was calculated by weighting each conduit by its contribution to Σd_V^4 by using the relationship $\Sigma d_V^5 / \Sigma d_V^4$ (Sperry and Saliendra 1994). K_P was calculated as described in equation 1 & 2 (Sterck *et al*. 2008, Poorter *et al*. 2010).

$$\mathrm{K}_P = \left(\pi_{P_w} \big/ 128_{\eta}\right) x.V_d\,.x.d_h^4 \qquad \text{Equation 1}$$

where, P_W = density of water at 20^{o}C = (998.2 kg m^{-3} at 20^{o}C*)* and η is the viscosity of water at 20^{o}C = (1.002 x 10^{-3} Pa s at 20^{o}C). V_d is vessel density, and d_h is the hydraulically-weighted vessel diameter (in m). Since vessels are not exactly circular, the diameter of each vessel was calculated as the mean of the minimum and maximum diameters. The average d_h was calculated as (Sterck *et al.*, 2008):

$$d_h = \left[\left(1\big/n\right)\sum_{i-1}^{n} d^4\right]^{1/4} \qquad \text{Equation 2}$$

Having measured potential hydraulic conductivity K_P, I then measured specific leaf area conductivity (K_L, kg m^{-1}s^{-1} MPa^{-1}) by multiplying K_P by its Huber value (H_V). K_P is higher than the true conductivity (K_S, kg m^{-1}s^{-1} MPa^{-1}) because the resistance of the vessel perforation plates and vessel endwalls which have significant hydraulic resistance (Sperry *et al*. 2006), and cavitated vessels are also excluded. An assumption is that these additional resistances will not significantly alter the observed species' ranking, such that K_S scales positively with K_P. I opted to using K_P instead of direct measurements of stem hydraulic conductivity because there were many different species, and it was difficult to estimate ionic concentration necessary to minimize interferences of the rate at which a given mass of water travels from the stem to leaf.

Huber value

Huber value (H_V, m^2/m^{-2}) is defined as xylem or sapwood cross-section (SA, m^2) area per unit leaf area (LA, m^2). H_V expresses the relative investment of xylem wood for a given amount of leaf area – a measure of shoot hydraulic cost. H_V was measured from 13 randomly selected mangrove species across zonation and the entire range of growth forms. To measure the sapwood area of the distal end of the branch supporting a given leaf area, I sliced thin sections (~0.1mm thick) with a fresh razor blade. I then measured mean SA of each species from $n = 10$ to calculate the H_V. To estimate H_V, 10 mature twigs (little branches) free of defective leaves were excised from sun branches and sealed in a zip lock bag and transported to the field laboratory. In the laboratory, I then measured the total leaf area (LA) of the twigs by removing all the leaves on the given twig and imaging the fresh leaves with portable Cannon scanner at 300 DPI. I then used ImageJ software to analyse the total LA (m^2). Corresponding SA (m^2) was measured from the distal end of the twig.

Theoretical leaf area specific hydraulic conductivity (K_L*)*

Leaf area specific hydraulic conductivity (K_L kg MPa $m^{-1}s^{-1}$), defined as a measure of the capacity of xylem to support a given leaf area (LA) was estimated through multiplying K_P by H_V (Brodribb and Feild 2000). K_L which is expressed as a ratio of K_H over LA was estimated from multiplying K_P x H_V (See my earlier explanation for reasons why.)

Because the values of K_P and H_V are known, the unknown K_L was calculated using the formula; $K_L=K_P$ x HV. The elaborated formula for $K_L = \frac{K_H}{SA} X \frac{SA}{LA} = K_P .X.H_V = \frac{K_H}{LA}$

RESULTS

Wood density trait (P_{wood}, g m^{-3}) varied among different zones and growth forms (Fig. 3.0, 3.1). P_{wood} varied across species within each zone and ranged from; 0.54 ± 0.02 SD g m^{-3} in *Sonneratia alba* to 0.94 ± 0.03 SD g m^{-3} in *Pemphis acidula* for the MLT zone, 0.55 ± 0.02 SD g m^{-3} in *Excoecaria agallocha* to 0.92 ± 0.0.05 SD g m^{-3} in *Rhizophora stylosa* for the MHT zone, 0.359 ± 0.02 SD g m^{-3} in *Dolichandrone spathacea* to 0.82 ± 0.02 SD g m^{-3} in *Scyphiphora hydrophyllacea* for the UHT zone, and 0.56 ± 0.03 SD g m^{-3} in *Cynometra ramiflora* to 0.73 ± 0.03 SD g m^{-3} in *Bruguiera cylindrica* for the BSM zone. The P_{wood} displayed variation across species and overlapped with adjoining zones (Fig.3.1). The maximum P_{wood} (0.94 ± 0.03 g m^{-3}) was recorded in *Pemphis acidulous*, and the minimum (0.359 ± 0.02 g m^{-3}) was recorded in *Dolichandrone spathacea* (Table 3.1).

An ANOVA showed significant differences in P_{wood} among zones ($F_{3,21} = 40.96$, $P < 0.001$). The PMC showed that P_{wood} for zone 2 versus zone 4; zone 3 versus zone 4; and zone 1 versus zone 4 all had significantly ($P < 0.001$) higher mean values. Mean P_{wood} values for “the other pairwise comparisons” were not significantly different (Table 3.0).

P_{wood} varied by over 30% among different growth forms (Fig. 3.1) and ranged from 0.56 ± 0.02 SD g m^{-3} in *Acanthus ilicifolius* to 0.94 ± 0.03 SD g m^{-3} in *Pemphis acidula* within the shrub growth forms, 0.55 ± 0.02 SD g m^{-3} in *Excoecaria agallocha* to 0.81 ± 0.04 SD g m^{-3} in *Bruguiera exaristata* within the small-medium tree growth forms, 0.35 ± 0.02 SD g m^{-3} in *Dolichandrone spathacea* to 0.92 ± 0.05 SD g m^{-3} in *Rhizophora stylosa* within the large tree growth form. The results of ANOVA on P_{wood} means showed that there were no significant differences among growth forms ($P > 0.05$, Table 3.0).

Table 3a: Summary of multiple pairwise comparison (Holm-Sidak method) post hoc analyses and linear correlation coefficient values. The abbreviations are: comparison = source variables, DM = difference of mean, t = t-test, Yes = two source variables have significant difference between means at $p < 0.05$, No = not significantly different, *F*-test = Fisher's value for one-way ANOVA, P_{wood} = wood density, Zn = zone, V_d = vessel density, d_V = vessel diameter, d_h = hydraulic diameter, grwthF = growth form, K_p = potential hydraulic conductivity, K_L – specific leaf area conductivity. P = threshold significance probability level (i.e. 0.05) and p = statistical probability value for given statistical t value.

Comparison	**DM**	**t**	**p**	***p* < 0.05**	***F*-test**	**P-value**
Pwoodzone2 vs. Pwoodzone4	0.71	9.68	0.001	Yes	$F_{3,21} = 10.96$	0.001
Pwoodzone3 vs. Pwoodzone4	0.69	9.43	0.001	Yes		0.001
Pwoodzone1 vs. Pwoodzone4	0.68	8.93	0.001	Yes		0.001
Pwoodzone2 vs. Pwoodzone1	0.03	0.47	0.64	No		0.64
Pwoodzone2 vs. Pwoodzone3	0.02	0.28	0.79	No		0.79
Pwoodzone3 vs. Pwoodzone1	0.01	0.21	0.84	No		0.84
Pwood vs. growthform				No	$F_{2,17} = 0.58$	0.57
PwoodRoot5 vs. PwoodRoot1	0.18	4.74	0.001	Yes	$F_{4,27} = 6.33$	0.001
PwoodRoot2 vs. PwoodRoot1	0.12	3.39	0.002	Yes		0.002
PwoodRoot4 vs. PwoodRoot1	0.13	3.36	0.003	Yes		0.003
PwoodRoot3 vs. PwoodRoot1	0.12	3.23	0.004	Yes		0.004
PwoodRoot5 vs. PwoodRoot3	0.06	1.66	0.11	No		1.66

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Comparison	**DM**	**t**	**p**	**P < 0.05**	**F-test**	**P-value**
PwoodRoot5 vs. PwoodRoot2	0.06	1.51	0.15	No		1.51
PwoodRoot5 vs. PwoodRoot4	0.05	1.32	0.2	No		1.32
PwoodRoot4 vs. PwoodRoot3	0.01	0.28	0.78	No		0.28
PwoodRoot2 vs. PwoodRoot3	0.01	0.16	0.87	No		0.16
PwoodRoot4 vs. PwoodRoot2	0.00	0.13	0.9	No		
VesdensZn1 vs. VesdensZn4	59.11	3.32	0.00	Yes	$F_{3,16} = 5.01$	0.01
VesdensZn1 vs. VesdensZn3	58.08	3.27	0.01	Yes		
VesdensZn1 vs. VesdensZn2	49.69	2.80	0.01	No		
VesdensZn2 vs. VesdensZn4	9.42	0.53	0.60	No		
VesdensZn2 vs. VesdensZn3	8.39	0.47	0.64	No		
VesdensZn3 vs. VesdensZn4	1.02	0.06	0.96	No		
Vesdens vs growth forms				No	$F_{2,15} = 1.66$	0.22
Vesdia vs. zonation				No	$F_{2,17} = 0.33$	0.72
Vesdiagrwth3 vs.Vesdiagrwth1	11.66	2.81	0.01	Yes	$F_{2,15} = 4.57$	0.03
Vesdiagrwth3 vs.Vesdiagrwth2	10.65	2.36	0.03	No		
Vesdiagrwth2 vs.Vesdiagrwth1	1.02	0.23	0.82	No		
Kp vs. Zonation					$F_{3,16} = 0.97$	0.43
Kp vs. growth forms					$F_{2,15} = 2.46$	0.119

Table 3b: Correlation between leaf and wood functional traits. Abbreviations are; LMA = leaf mass per area (g m^{-2}), P_{wood} = wood density (g m^{-3}), V_d = vessel density (number of vessel m^{-2}), d_V = vessel diameter (mm), K_P = Potential specific area hydraulic conductivity (kg $m^{-1}s^{-1}MPa^{-1}$), K_L = Calculated specific leaf area conductivity (kg $m^{-1}s^{-1}MPa^{-1}$), A_{max} = Maximum light photosynthetic carbon assimilation rate (µmol $CO^2m^{-1}s^{-1}$), R^2 = pearson's correlation coefficient value.

Correlation	**R^2 -value**	**P-value**
LMA vs. P_{wood}	$R^2 = 0.10$	$P > 0.08$
V_d vs. d_V	$R^2 = -0.18$	$P < 0.02$
d_h vs. V_d	$R^2 = -0.22$	$P < 0.01$
K_P vs. D_V	$R^2 = 0.001$	$P > 0.05$
K_L vs. D_V	$R^2 = 0.47$	$P < 0.05$
K_L vs. A_{max}	$R^2 = 0.55$	$P < 0.05$

Relationship between leaf mass area and wood density

LMA was not correlated with P_{wood} across the 30 speciesof New Guinean mangroves ($R^2 = 0.10$, $P > 0.09$; Fig.3.8). *Pemphis acidula* had the highest P_{wood} (0.94 ± 0.03 g m^{-3}) and LMA (289 ± 5.60 g m^{-2}). *Acanthus ilicifolius* had the lowest P_{wood} (0.56 ± 0.02 g m^{-3}). About 63% of the high P_{wood} (> 0.80 g m^{-3}) species had corresponding high LMA (> 150 g m^{-2}).

Table 3.1: Summary of wood density traits showing maximum, minimum, and mean P_{wood} (g m^{-3}) at different zones, growth forms, and root system types. Where, MLT = mean low tide zone, MHT = medium high tide zone, UHT = upper high tide zone, and BSM = back swamp mangrove zone.

Zones	**P_{wood}Max (g m^{-3})**	**P_{wood}Min (g m^{-3})**	**P_{wood}Mean (g m^{-3})**
MLT	0.94 ± 0.03	0.54 ± 0.02	0.73 ± 0.02
MHT	0.92 ± 0.05	0.55 ± 0.02	0.71 ± 0.03
UHT	0.82 ± 0.02	0.36 ± 0.03	0.68 ± 0.03
BSM	0.73 ± 0.03	0.56 ± 0.03	0.64 ± 0.02
Growth Forms			
Shrubs	0.94 ± 0.03	0.56 ± 0.02	0.74 ± 0.06
Small-medium Trees	0.81 ± 0.04	0.55 ± 0.02	0.72 ± 0.03
Large Trees	0.92 ± 0.02	0.35 ± 0.02	0.67 ± 0.04
Root System Types			
Unbuttressed (# 1)	0.94 ± 0.03	0.55 ± 0.02	0.70 ± 0.04
Stilt/Prop root (# 5)	0.69 ± 0.03	0.54 ± 0.02	0.61 ± 0.04
Knee-like root (# 3)	0.81 ± 0.04	0.35 ± 0.02	0.71 ± 0.03
Pneumatophore (# 2)	0.82 ± 0.04	0.66 ± 0.01	0.76 ± 0.04
Plank buttresses (#4)	0.92 ± 0.05	0.36 ± 0.03	0.70 ± 0.04

Table 3.2: Summary of vessel density traits showing maximum, minimum, and mean vessel density (number of vessels mm^{-2}) at different zones, growth forms, and root system types. Where, MLT = mean low tide zone, MHT = medium high tide zone, UHT = upper high tide zone, and BSM = back swamp mangrove zone.

Zones	**$V_d$min**	**$V_d$max**	**$V_d$mean**
MLT	46.46 ± 3.92	346.46 ± 6.46	128.49 ± 6.46
MHT	42.85 ± 9.56	130.92 ± 14.28	73.51 ± 3.26
UHT	12.66 ± 2.61	108.58 ± 12.87	51.47 ± 2.47
BSM	33.86 ± 4.94	64.51 ± 3.91	51.31 ± 3.46
Growth forms			
Shrubs	46.46 ± 3.92	346.46 ± 6.46	113.44 ± 5.30
Small-medium trees	57.31 ± 6.82	108.58 ± 6.82	74.74 ± 6.17
Large trees	12.66 ± 2.61	130.92 ± 14.28	56.17 ± 6.54
Root System Types			
Unbuttressed	15.80 ± 4.32	346.46 ± 6.46	86.38 ± 4.9
Stilt-prop root	32.54 ± 3.54	116.20 ± 6.93	71.25 ± 3.06
Knee-like root	51.58 ± 4.38	128.51.58 ± 5.99	78.35 ± 6.5
Pneumatophore	31.01 ± 9.14	130.93 ± 14.28	57.52 ± 5.54
Plank buttresses	12.66.86 ± 2.61	63.83 ± 5.93	42.35 ± 5.03

Table 3.3: Summary of wood anatomy traits showing maximum, minimum, and mean d_V for different zones, growth forms, and root system types. Where, MLT = mean low tide zone, MHT = medium high tide zone, UHT = upper high tide zone, BSM = back swamp mangrove zone, $d_V$max = maximum vessel diameter, $V_d$min = minimum vessel density, $V_d$max= maximum vessel density, $d_h$min = minimum hydraulic diameter, and $d_h$max = maximum hydraulic diameter.

Zones	**$d_V$min**	**$d_V$max**	**$d_V$mean**
MLT	28.23 ± 5.77	63.73 ± 11.91	57.49 ± 16.39
MHT	39.27 ± 12.29	72.40 ± 22.31	38.83 ± 12.44
UHT	30.84 ± 12.32	72.46 ± 22.31	48.85 ± 12.82
BSM	41.52 ± 11.01	74.45 ± 22.04	52.99 ± 11.28
Growth Forms			
Shrubs	28.23 ± 5.77	54.10 ± 12.45	55.02 ± 17.88
Small-medium trees	37.41 ± 9.47	72.40 ± 22.31	38.21 ±9.02
Large trees	30.84 ± 12.32	74.45 ± 22.04	12.32 ±2.32
Root System Types			
Unbuttressed	30.03 ± 5.77	83.39 ± 11.91	46.56 ± 13.46
Stilt-prop root	12.66 ± 12.29	130.93 ± 22.31	53.61 ± 13.32
Knee-like root	15.80.84 ± 12.32	84.02± 22.31	50.58 ± 14.31
Pneumatophore	51.58 ± 11.01	116.20 ± 22.04	40.55 ± 10.90
Plank buttresses	32.54 ± 11.02	108.58 ± 22.05	50.47 ± 13.40

Table 3.4: Summary of wood anatomy traits showing maximum, minimum, and mean d_h for different zones, growth forms, and root system types. Where, MLT = mean low tide zone, MHT = medium high tide zone, UHT = upper high tide zone, BSM = back swamp mangrove zone, $d_h$min = minimum hydraulic diameter, $d_h$max = maximum hydraulic diameter, $d_h$mean = mean hydraulic diameter.

Zones	**$d_h$min**	**$d_h$max**	**$d_h$mean**
MLT	45.81 ± 5.77	71.81 ± 11.91	128.49 ± 6.46
MHT	49.83.27 ± 12.29	92.12 ± 22.31	73.51 ± 3.26
UHT	38.55 ± 12.32	91.47 ± 22.31	51.47 ± 2.47
BSM	50.45 ± 11.01	92.56 ± 22.04	51.31 ± 3.46
Growth forms			
Shrubs	38.55 ± 5.77	62.81 ± 11.91	113.44 ± 5.30
Small-medium trees	45.18.27 ± 12.29	92.12 ± 22.31	74.74 ± 6.17
Large trees	45.99 ± 12.32	92.56 ± 22.31	56.17 ± 6.54
Root System Types			
Unbuttressed	38.55 ± 5.77	92.56 ± 11.91	86.38 ± 4.9
Stilt-prop root	41.96 ± 12.29	87.52 ± 22.31	71.25 ± 3.06
Knee-like root	45.18 ± 12.32	91.47 ± 22.31	78.35 ± 6.5
Pneumatophore	45.24 ± 11.01	71.81 ± 22.04	57.52 ± 5.54
Plank buttresses	45.99 ± 11.01	92.12 ± 22.04	42.35 ± 5.03

Relationship between Root System Types and Wood density

Examination of the relationship between root system type (RST) and wood density (P_{wood}, g m^{-3}) showed marked variation in P_{wood} among the different root types (Fig. 3.3, Table 3.1). P_{wood} varied markedly within the 'pencil-like' and 'plank-buttresses' RST; varied by two-fold within the 'no aerial' and 'Knee-like' RST; and by three-fold within the stilt/prop RST. The P_{wood} ranged from 0.55 ± 0.02 SD g m^{-3} in *Excoecaria agallocha* to 0.94 ± 0.03 SD g m^{-3} in *Pemphis acidula* for the 'no aerial' RST, 0.54 ± 0.02 SD g m^{-3} in *Sonneratia alba* to 0.69 ± 0.0.03 SD g m^{-3} in *Avicennia marina* for the 'pencil-like' RST, 0.35 ± 0.02 SD g m^{-3} in *Dolichandrone spathacea* to 0.81 ± 0.04 SD g m^{-3} in *Bruguiera exaristata* for the 'knee-like' RST, 0.66 ± 0.01 SD g m^{-3} in *Xylocarpus granatum* to 0.82 ± 0.04 SD g m^{-3} in *Xylocarpus australasicus* for the plank-buttresses RST, and 0.36 ± 0.03 SD g m^{-3} in *Myristica hollrungii* to 0.92 ± 0.05 SD g m^{-3} in *Rhizophora stylosa* for the 'stilt/prop'.

An ANOVA showed highly significant differences in P_{wood} among different root system types ($F_{4,27} = 6.33$, $P < 0.001$). The PMC showed that P_{wood} varied significantly for RST 1 versus all other RSTs (Table 3.0).

Relations between Vessel density, Zonation, and Growth forms

Vessel density trait (V_d, number of vessel mm^{-2}) varied among different zones and growth forms (Fig. 3.4, 3.5). Vessel density varied by ~ eight-fold across species in the MLT zone, ~ three-fold in the MHT zone, ~ nine-fold in the UHT zone, and ~ two-fold in the BSM zone. The V_d differences ranged from 46.46 ± 3.92 SD number of vessel mm^{-2} in *Aegilitis annulata* to 346.06 ± 6.46 SD number of vessel mm^{-2} in *Aegiceras corniculatum* for the MLT zone, 42.85 ± 9.56 SD number of vessel mm^{-2} in *Rhizophora apiculata* to 130.92 ± 14.28 SD number of vessel mm^{-2} in *Xylocarpus australasicus* for the MHT zone, 12.66 ± 2.61 SD number of vessel mm^{-2} in *Myristica hollrungii* to 108.58 ± 12.87 SD number of vessel mm^{-2} in *Bruguiera exaristata* for the UHT zone, and 33.86 ± 4.94 SD number of vessel mm^{-2} in *Cynometra ramiflora* to 64.51 ± 3.91 SD number of vessel mm^{-2} in *Stemonurus apiculus* for the BSM zone. The V_d range for each zone overlapped with adjoining zones (Fig. 3.4). The maximum V_d (346.06 ± 6.46 number of vessel mm^{-2}) was recorded in *Aegiceras corniculatum* and the minimum (12.66 ± 2.61 number of vessel mm^{-2}) was recorded in *Myristica hollrungii* (Table 3.1).

An ANOVA showed significant differences in V_d among the four growth zones ($F_{3,16} = 5.01$, $P < 0.01$). Pairwise multiple comparisons (PMC) (Holm-Sidak method) post hoc analyses indicated how these growth zones differed. The PMC showed that V_d between zone 1 versus zone 4 and zone 1 versus zone 3 had significantly ($P < 0.01$) higher mean differences. The mean differences of zone 1 versus zone 2, zone 2 versus zone 4, zone 2 versus zone 3, and zone 3 versus zone 4 were not significantly different (Table 3.0).

The V_d varied among different growth forms (Fig. 3.5); by seven-fold across shrub ranging from 46.46 ± 3.92 SD number of vessel mm^{-2} in *Aegilitis annulata* to 346.06 ± 6.46 SD number of vessel mm^{-2} in *Aegicerus corniculatum*; by two-fold across small-medium tree ranging from 57.31 ± 0.82 SD number of vessel mm^{-2} in *Ceriops tagal* to 108.58 ± 12.87 number of vessel mm^{-2}, and by 10-fold across large trees ranging from 12.66 ± 2.61 SD number of vessel mm^{-2} in *Myristica hollrungii* to 130.92 ± 14.28 (Table 3.1). An ANOVA on mean V_d. among the different growth forms was not significant ($F_{2,15}$ = 1.66, P > 0.05, Table 3.0).

Relations between Vessel diameter, Zonation, and Growth forms

The vessel diameter (d_V µm) trait varied among different zones and growth forms (Fig. 3.6, 3.7). Vessel diameter varied by ~ two-fold across species in all four (MLT, MHT, UHT, and BSM) zones. The d_V differences ranged from 28.23 ± 5.77 SD µm in *Aegiceras corniculatum* 63.73 ± 11.91 SD µm in *Sonneratia alba* for the MLT zone, 39.27 ± 12.29 SD µm in *Xylocarpus austalasicus* to 72.40 ± 22.31 SD µm in *Excoecaria agallocha* for the MHT zone, 30.84 ± 12.32 SD µm in *Avicennia alba* to 72.46 ± 22.31 SD µm in *Dolichandrone spathacea* for the UHT zone, and 41.52 ± 11.01 SD µm in *Stemonurus apicalis* to 74.45 ± 22.04 SD µm in *Cynometra ramiflora* for the BSM zone. The d_V range for each zone overlapped with adjoining zones (Fig. 3.6). The maximum

d_V (74.45 ± 22.04 µm) was recorded in *Cynometra ramiflora*, and the minimum 28.23 ± 5.77 SD µm occurred in *Aegiceras corniculatum* (Table 3.1). However, an ANOVA showed no significant differences in d_V among zones ($F_{2,15} = 1.66$, $P > 0.05$).

Vessel diameter varied by ~ two-fold across species in the shrub and small-medium tree growth forms and by ~ three-fold in the large tree growth form. The d_V differences ranged from 28.23 ± 5.77 SD µm in *Aegiceras corniculatum* to 54.10 ± 12.45 SD µm in *Pemphis acidula* for the shrub growth form, 37.41 ± 9.47 SD µm in *Ceriops decandra* to 72.40 ± 22.31 SD µm in *Excoecaria agallocha* for the small-medium tree growth form, and 30.84 ± 12.32 SD µm in *Avicennia alba* to 74.45 ± 22.04 SD µm in *Cynometra ramiflora* for the large tree growth form. The d_V range for each zone overlapped with adjoining zones (Fig. 3.6). The maximum d_V (74.45 ± 22.04 µm) was recorded in a tree species (*Cynometra ramiflora*) and the minimum (28.23 ± 5.77 SD µm) was recorded in a shrub species (*Aegiceras corniculatum* (Table 3.1).

An ANOVA showed significant differences in d_V among different growth forms ($F_{2,15} = 4.57$, $P < 0.03$). Post hoc analyses showed that d_V between growth form 3 versus zone 1 had a significantly ($P < 0.03$) higher mean difference. The mean differences of growth form 2 versus growth form 1 and growth form 3 versus growth form 2 were not significantly different (Table 3.0).

Relationship between Vessel density and Vessel diameter

A linear correlation of vessel density (V_d) and vessel diameter (d_V) for 30 species (Fig. 3.8) displayed a significant inverse relationship ($R^2 = 0.18$, $P < 0.02$). As vessel diameter increased, vessel density decreased. Species with large vessel diameter and low vessel density included the following: *Dolichandrone spathacea, Myristica hollrungii, Heritiera littoralis, and Cynometra ramiflora,* and those with high vessel density and low vessel diameter included the following: *Xylocarpus autralasicus, Osbornia octodonta, Sonnerratia alba,* and *Bruguiera exaristata*.

Relationship between Hydraulic mean diameter and Vessel density.

A linear correlation of vessel density (V_d) and hydraulic mean diameter (d_h) for 30 species (Fig. 3.9) also displayed a significant inverse relationship ($R^2 = 0.22$, $P < 0.01$). As d_h (µm) increased, V_d (number of vessels mm^{-2}) decreased. Species having large d_h (*Dolichandrone spathacea, Myristica hollrungii, Cynometra ramiflora,* and *Heritiera littoralis*) had corresponding low V_d, and species with high V_d (*Osbornia octodonta, Xylocarpus australasicus, Bruguiera exaristata*) had corresponding low d_h.

Relationship between Potential hydraulic Conductivity, Zonation and Growth forms

Potential hydraulic conductance (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) varied among different zones and growth forms (Fig. 3.11, 3.12). K_P varied by ~ five-fold across species in MLT, ~three-fold in MHT, ~five-fold in UHT, and ~three-fold in BSM zones. The K_P differences ranged from 22.65 kg $m^{-1}s^{-1}MPa^{-1}$ in *Aegiceras corniculatum* to 112.75 kg $m^{-1}s^{-1}MPa^{-1}$ in *Sonneratia alba* for the MLT zone, 49.66 kg $m^{-1}s^{-1}MPa^{-1}$ in *Acanthus ilicifolius* to 164.31 kg $m^{-1}s^{-1}MPa^{-1}$ in *Excoecaria agallocha* for the MHT zone, 30.65 kg $m^{-1}s^{-1}MPa^{-1}$ in *Lumnitzera racemosa* to 162.60 kg $m^{-1}s^{-1}MPa^{-1}$ in *Dolichandrone spathacea* for the UHT zone, and 51.61 kg $m^{-1}s^{-1}MPa^{-1}$ in *Stemonurus apicalis* to 169.76 kg $m^{-1}s^{-1}MPa^{-1}$ in *Cynometra ramiflora* for the BSM zone. The maximum K_P (169.76 kg $m^{-1}s^{-1}MPa^{-1}$) was recorded in *Cynometra ramiflora*, and the minimum 22.65 kg $m^{-1}s^{-1}MPa^{-1}$ existed in *Aegiceras corniculatum* (Table 3.1). There were no significant differences in K_P among the zones ($F_{2,16} = 1.71$, $P > 0.05$).

Potential hydraulic conductance (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) varied among different growth forms (Fig. 3.12). K_P varied by ~ four-fold across shrubby species, ~four-fold in small-medium trees, and ~five-fold across the large trees. The K_P differences ranged from 22.65 kg $m^{-1}s^{-1}MPa^{-1}$ in *Aegiceras corniculatum* to 83.71 kg $m^{-1}s^{-1}MPa^{-1}$ in *Pemphis acidula* across the shrubby growth form, 41.70 kg $m^{-1}s^{-1}MPa^{-1}$ in *Ceriops decandra* to 164.31 kg $m^{-1}s^{-1}MPa^{-1}$ in *Excoecaria agallocha* across the small-medium tree growth form, and 34.94 kg $m^{-1}s^{-1}MPa^{-1}$ in *Avicennia alba* to 169.76 kg $m^{-1}s^{-1}MPa^{-1}$ in *Cynometra* *ramiflora* across the large tree growth form (Table 3.1). There were no significant differences in K_P among zones ($F_{2,15} = 2.46$, $P > 0.05$).

Relationship among Leaf photosynthetic and Wood Hydraulic Traits

A linear regression analysis of potential hydraulic conductivity (K_P) against vein density (D_V) for 29 species (Fig. 3.13) showed no significant regression ($y = 0.35x + 73.16$, $R^2 = 0.001$, $P > 0.05$) indicating no relation between D_V (mm mm^{-2}) and K_P (kg m^{-1}s^{-1}MPa^{-1}). Linear regression analysis of leaf specific area conductivity (K_L) against vein density showed a statistically significant regression ($y = 260.36x + 6.13$, $R^2 = 0.47$, $P < 0.05$) indicating a relationship between D_V (mm mm^{-2}) and K_L (kg m^{-1}s^{-1}MPa^{-1}) (Fig. 2.14). Analysis of linear correlation coefficient of leaf area specific conductivity and maximum photosynthetic carbon assimilation rate showed a positive correlation ($R^2 = 0.55$, $P < 0.004$) indicating a link between A_{max} (µmol CO_2 m^{-2}s^{-1}) and K_L (kg m^{-1}s^{-1}MPa^{-1}) (Fig. 2.15).

Relationship of Potential Hydraulic Conductivity to Vessel density and Vessel diameter

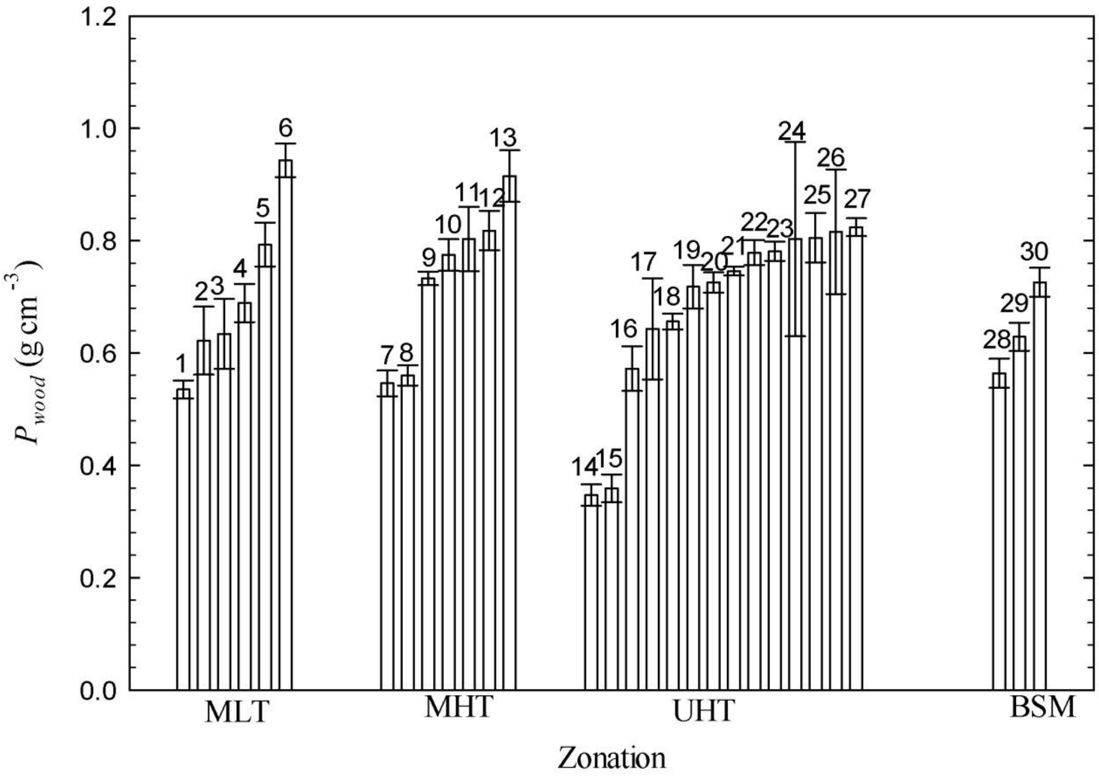
Examination of a relationship between potential hydraulic conductivity (K_P, kg $m^{-2}s^{-1}MPa^{-1}$) and vessel density (V_d, number of vessels mm^{-2}) showed an inverse correlation ($R^2 = 0.21$, $P < 0.01$). Hydraulic conductivity decreased steadily with increasing vessel density (Fig. 3.16). Highest K_P values were observed in species with low vessel densities (*Avicennia officinalis*, *Heritiera littoralis*, *Dolichandrone spathacea*, *Cynometra ramiflora*, *Myristica hollrungii*), and low K_P values were observed in species with high V_d (*Avicennia alba*, *Avicennia marina*, *Luminitzera racemosa*, *Scyphiphora hydrophyllacea*).

Examination of the relationship between potential hydraulic conductivity (K_P, kg $m^{-2}s^{-1}MPa^{-1}$) and vessel diameter (d_V, µm) showed a strong positive correlation ($R^2 = 0.95$, $P < 0.0001$). Xylem area specific hydraulic conductivity increased with d_V (Fig. 3.17. High K_P was observed in the species with high vessel diameter (*Sonneratia alba*, *Avicennia officinalis*, *Heritiera littoralis*, *Myristica hollrungii*, *Dolichandrone spathacea*, *Excoecaria agallocha*, *Cynometra ramiflora*) and low K_P values were observed in low d_V species (*Aegiceras corniculatum*, *Luminitzera racemosa*, *Avicennia alba*, *Scyphiphora hydrophyllacea*).

Correlation between Potential Hydraulic Conductivity and Vessel mean Hydraulic diameter

Examination of a relationship between potential hydraulic conductivity (K_P, kg $m^{-2}s^{-1}MPa^{-1}$) and weighted hydraulic mean diameter (d_h, µm) revealed a positive correlation ($R^2 = 0.78$, $P < 0.0001$). Xylem area specific hydraulic conductivity increased with increasing d_h (Fig.3.18). High K_P was observed in species with high d_h (*Sonneratia alba*, *Avicennia officinalis*, *Heritiera littoralis*, *Myristica hollrungii*, *Dolichandrone spathacea*, *Excoecaria agallocha*, *Cynometra ramiflora*) and low K_P values were observed in low d_h species (*Aegiceras corniculatum*, *Luminitzera racemosa*, *Avicennia alba, Scyphiphora hydrophyllacea*).

Figure 3.0. Variation in wood density (P_{wood}) across community zonations (MLT= Mean Low Tide, MHT=Medium High Tide, UHT=Upper High Tide) in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Sonneratia alba*, 2 = *Aegiceras corniculatum,* 3 = *Aegilitis annulata,* 4 = *Avicennia marina,* 5 = *Osbornia octodonta*, 6 = *Pemphis acidula,* 7 = *Excoecaria agallocha,* 8 = *Acanthus ilicifolius*, 9 = *Rhizophora mucronata*, 10 = *Bruguiera gymnorhiza*, 11 = *Rhizophora apiculata*, 12 = *Xylocarpus australasicus,* 13 = *Rhizophora stylosa*, 14 = *Dolichandrone spathacea*, 15 = *Myristica hollrungii*, 16 = *Avicennia officinalis,* 17 = *Avicennia alba*, 18 = *Xylocarpus granatum*, 19 = *Bruguiera parviflora,* 20 = *Bruguiera sexangula,* 21 = *Heritiera littoralis,* 22 = *Ceriops decandra,* 23 = *Ceriops tagal*, 24 = *Luminitzera racemosa,* 25 = *Bruguiera exaristata,* 26 = *Xylocarpus rumphii*, 27 = *Scyphiphora hydrophyllacea*, 28 = *Cynometra ramiflora,* 29 = *Stemoneurus apicalis,* 30 = *Bruguiera cylindrica.*


P_{wood} (g cm $^{-3}$)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
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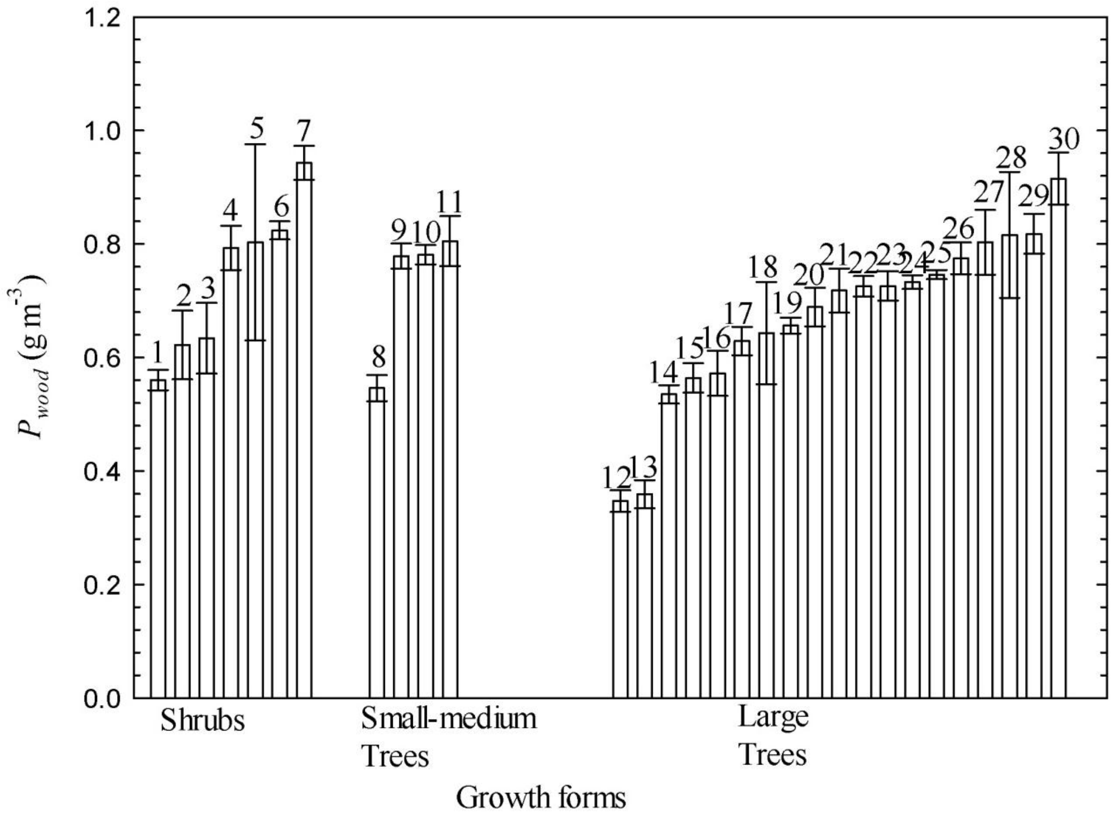
28
29
30
MLT
MHT
UHT
BSM
Zonation

Figure 3.0.

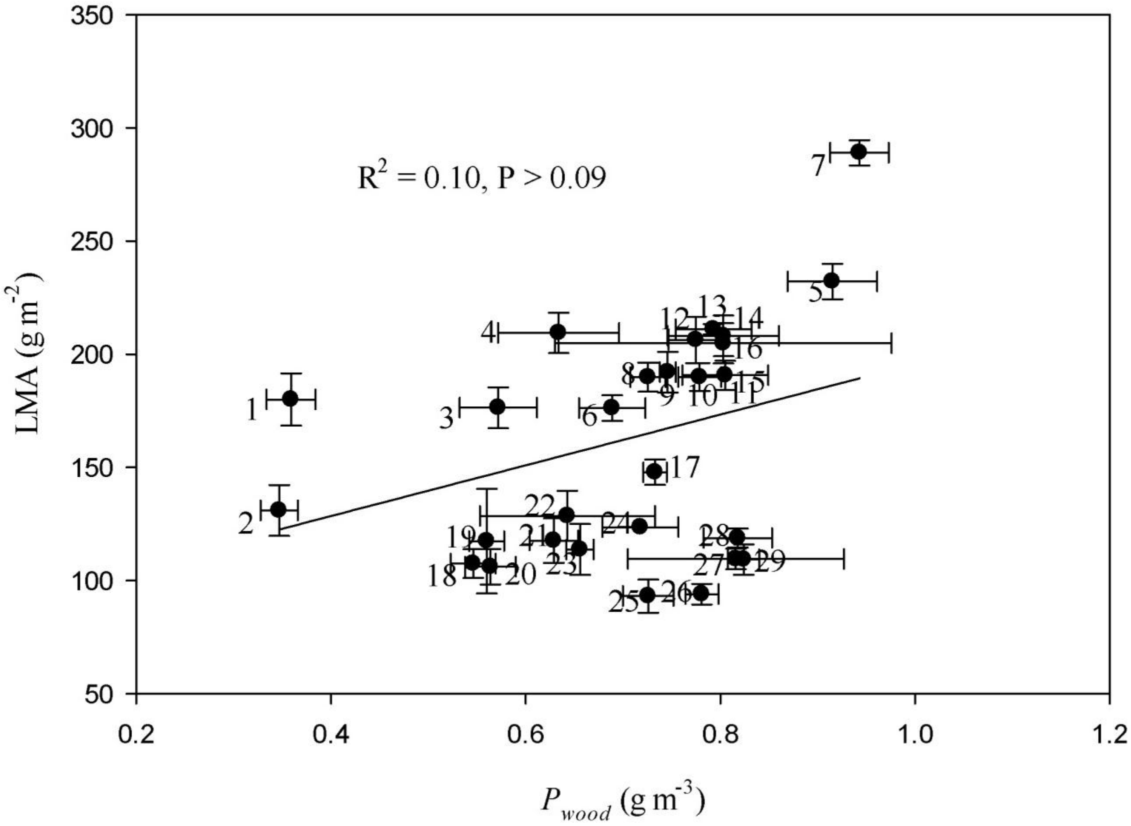
Figure 3.1. Variation in wood density (P_{wood}) among different growth forms (Shrubs, Small-medium Trees, Large Trees) in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Acanthus ilicifolius,* 2 = *Aegiceras corniculatum*, 3 = *Aegilitis annulata,* 4 = *Osbornia octodonta*, 5 = *Luminitzera racemosa*, 6 = *Scyphiphora hydrophyllacea,* 7 = *Pemphis acidula,* 8 = *Excoecaria agallocha,* 9 = *Ceriops decandra*, 10 = *Ceriops tagal*, 11 = *Bruguiera exaristata*, 12 = *Dolichandrone spathacea*, 13 = *Myristica hollrungii*, 14 = *Sonneratia alba*, 15 = *Cynometra ramiflora,* 16 = *Avicennia officinalis,* 17 = *Stemoneurus*, 18 = *Avicennia alba*, 19 = *Xylocarpus granatum*, 20 = *Avicennia marina*, 21 = *Bruguiera parviflora*, 22 = *Bruguiera sexangula*, 23 = *Bruguiera cylindrica*, 24 = *Rhizophora mucronata*, 25 = *Heritiera littoralis*, 26 = *Bruguiera gymnorhiza,* 27 = *Rhizophora apiculata*, 28 = *Xylocarpus rumphii*, 29 = *Xylocarpus australasicus,* 30 = *Rhizophora stylosa*.



1.2
1.0
0.8
0.6
0.4
0.2
0.0
P_{wood} (g m^{-3})
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Shrubs
Small-medium Trees
Large Trees
Growth forms

Figure 3.1.

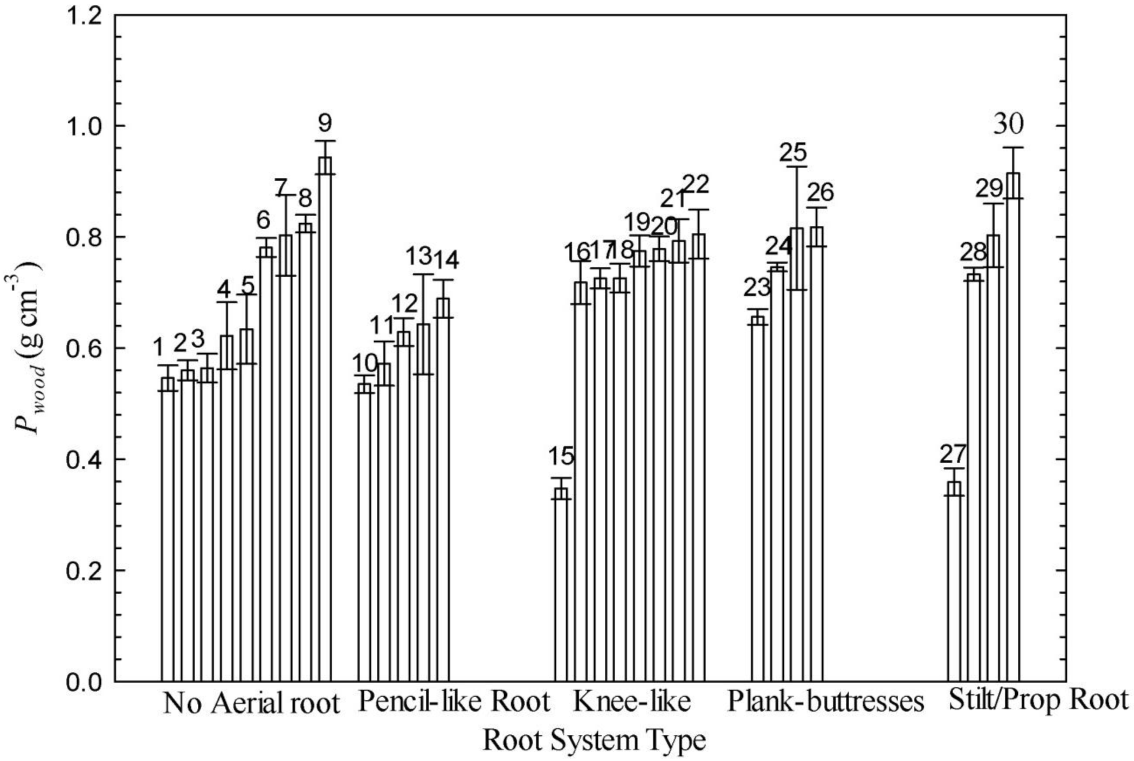
Figure 3.2. Correlation between leaf mass area (LMA, g m^{-2}) and wood density (P_{wood}, g m^{-3}) of 29 New Guinea mangrove species. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows; 1 = *Acanthus ilicifolius,* 2 = *Aegilitis annulata,* 3 = *Avicennia alba,* 4 = *Avicennia marina,* 5 = *Rhizophora stylosa,* 6 = *Bruguiera cylindrica,* 7 = *Pemphis acidula,* 8 = *Bruguiera gymnorhiza,* 9 = *Bruguiera parviflora,* 10 = *Ceriops decandra*, 11 = *Ceriops tagal,* 12 = *Cynometra ramiflora*, 13 = *Luminitzera racemosa*, 14 = *Rhizophora apiculata*, 15 = *Excoecaria agallocha,* 16 = *Heritiera littoralis,* 17 = *Dolichandrone spathacea*, 18 = *Myristica hollrungii,* 19 = *Osbornia octodonta,* 20 = *Bruguiera exaristata*, 21 =*Aegiceras corniculatum*, 22 = *Rhizophora mucronata,* 23 = *Avicennia officinalis,* 24 = *Scyphiphora hydrophyllacea,* 25 = *Sonneratia alba,* 26 = *Stemoneurus apiculus*, 27 = *Xylocarpus australasicus,* 28 = *Xylocarpus granatum,* 29 = *Xylocarpus rumphii*. Correlation curve show a positive relationship between LMA and P_{wood}, however, not statistically significant ($R^2 = 0.10$, $P > 0.09$).



R^2 = 0.10, P > 0.09
LMA (g m^{-2})
P_{wood} (g m^{-3})
350
300
250
200
150
100
50
0.2
0.4
0.6
0.8
1.0
1.2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

Figure 3.2.

Figure 3.3. Variation in wood density (P_{wood}) among different rooting types in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1= *Excoecaria agallocha*, 2 = *Acanthus ilicifolius,* 3 = *Dolichandrone spathacea*, 4 = *Aegiceras corniculatum*, 5 = *Aegilitis annulata*, 6 = *Cynometra ramiflora*, 7 = *Luminitzera racemosa*, 8 = *Scyphiphora hydrophyllacea*, 9 = *Pemphis acidula*, 10 = *Sonneratia alba*, 11 = *Avicennia officinalis*, 12 = *Stemonurus apicalis*, 13 = *Avicennia alba*, 14 = *Avicennia marina,* 15 = *Dolichandrone spathacea*, 16 = *Bruguiera parviflora*, 17 = *Ceriops decandra*, 18= *Brugueira cylindrica*, 19 = *Brugueira gymnorrhiza*, 20 = *Ceriops tagal*, 21 = *Osbornia octodonta*, 22 = *Brugueira exaristata*, 23 = *Xylocarpus granatum*, 24 = *Heritiera littoralis*, 25= *Xylocarpus rumphii*, 26= *Xylocarpus australasicus*, 27= *Myristica hollrungii,* 28 = *Rhizophora mucronata*, 29 = *Rhizophora apiculata*, 30 = *Rhizophora stylosa*



1.2
1.0
0.8
0.6
0.4
0.2
0.0
P_{wood} (g cm^{-3})
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
No Aerial root
Pencil-like Root
Knee-like
Plank-buttresses
Stilt/Prop Root
Root System Type

Figure 3.3.

Figure 3.4. Variation in vessel density (V_d) among different rooting types in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Aegilitis annulata*, 2 = *Pemphis acidula*, 3 = *Avicennia marina*, 4 = *Sonneratia alba*, 5 = *Osbornia octodonta*, 6 = *Aegiceras corniculatum*, 7 = *Rhizophora apiculata*, 8 = *Rhizophora stylosa*, 9 = *Excoecaria agallocha*, 10 = *Rhizophora mucronata*, 11 = *Acanthus ilicifolius*, 12 = *Brugueira gymnorrhiza*, 13 = *Xylocarpus australasicus*, 14 = *Myristica hollrungi*, 15 = *Dolichandrone spathacea*, 16 = *Heritiera littoralis*, 17 = *Xylocarpus granatum*, 18 = *Avicennia officinalis*, 19 = *Xylocarpus rumphii*, 20 = *Bruguiera sexangula*, 21 = *Ceriops tagal*, 22 = *Avicennia alba*, 23 = *Luminitzera racemosa*, 24 = *Bruguiera parviflora*, 25 =*Ceriops decandra*, 26 = *Scyphiphora hydrophyllacea*, 27 = *Bruguiera exaristata*, 28 = *Cynometra ramiflora*, 29 = *Bruguiera cylindrica*, 30 = *Stemonurus apicalis*.

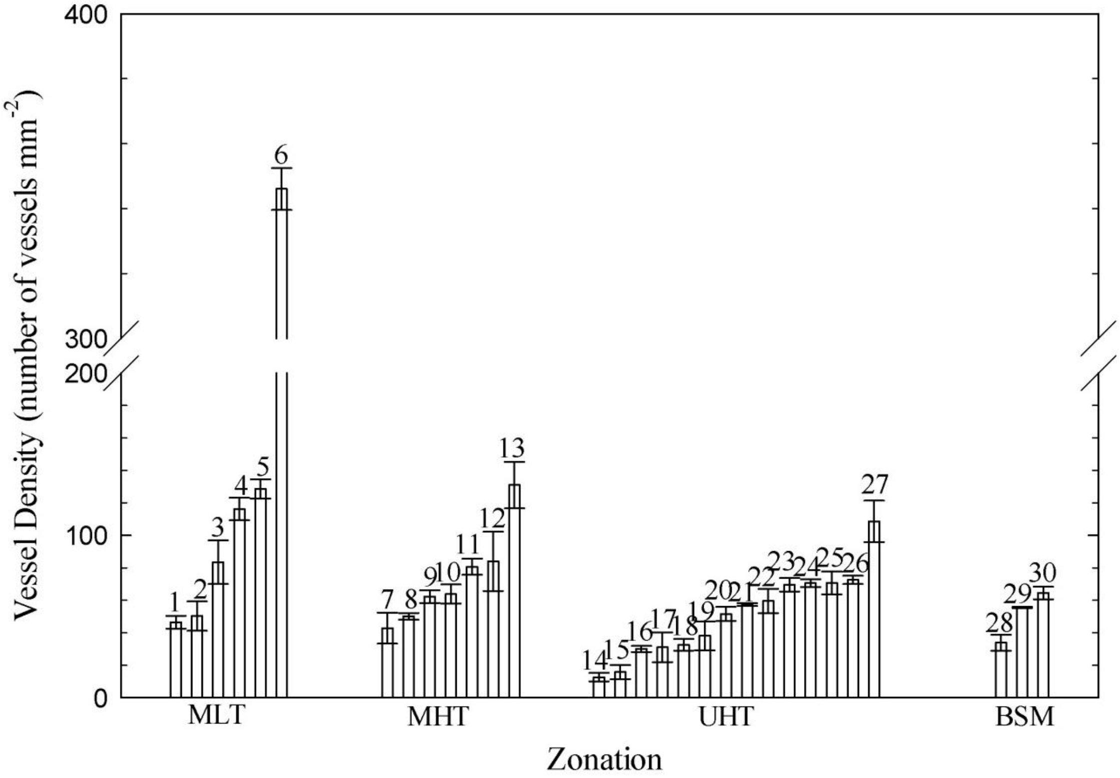

400
300
200
100
0
Vessel Density (number of vessels mm^{-2})
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
MLT
MHT
UHT
BSM
Zonation

Figure 3.4.

Figure 3.5. Variation in vessel density (V_d) among different rooting types in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Aegilitis annulata*, 2 = *Pemphis acidula*, 3 = *Luminitzera racemosa*, 4 = *Scyphiphora hydrophyllacea*, 5 = *Acanthus ilicifolius*, 6 = *Osbornia octodonta*, 7 = *Aegiceras corniculatum*, 8 = *Ceriops tagal*, 9 = *Excoecaria agallocha*, 10 = *Ceriops decandra*, 11 = *Brugueira exaristata*, 12 = *Myristica hollrungii*, 13 = *Dolichandrone spathacea*, 14 = *Heritiera littoralis*, 15 = *Xylocarpus granatum*, 16 = *Avicennia officinalis*, 17 = *Cynometra ramiflora*, 18 = *Xylocarpus rumphii*, 19 = *Rhizophora apiculata*, 20 = *Rhizophora stylosa*, 21 = *Bruguiera sexangula*, 22 = *Bruguiera cylindrica*, 23 = *Avicennia alba*, 24 = *Rhizophora mucronata*, 25 = *Stemonurus apicalis*, 26 =*Bruguiera parviflora*, 27 = *Avicennia marina*, 28 = *Brugueira gymnorrhiza*, 29 = *Sonneratia alba*, 30= *Xylocarpus australasicus.*

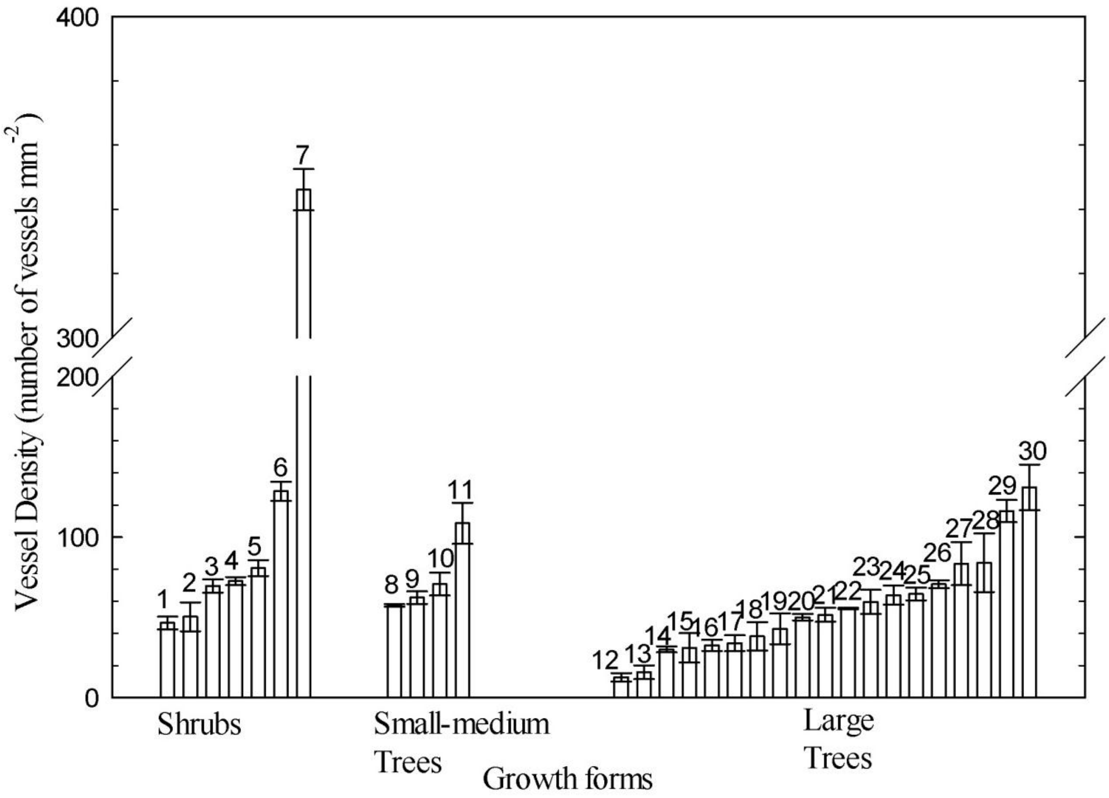
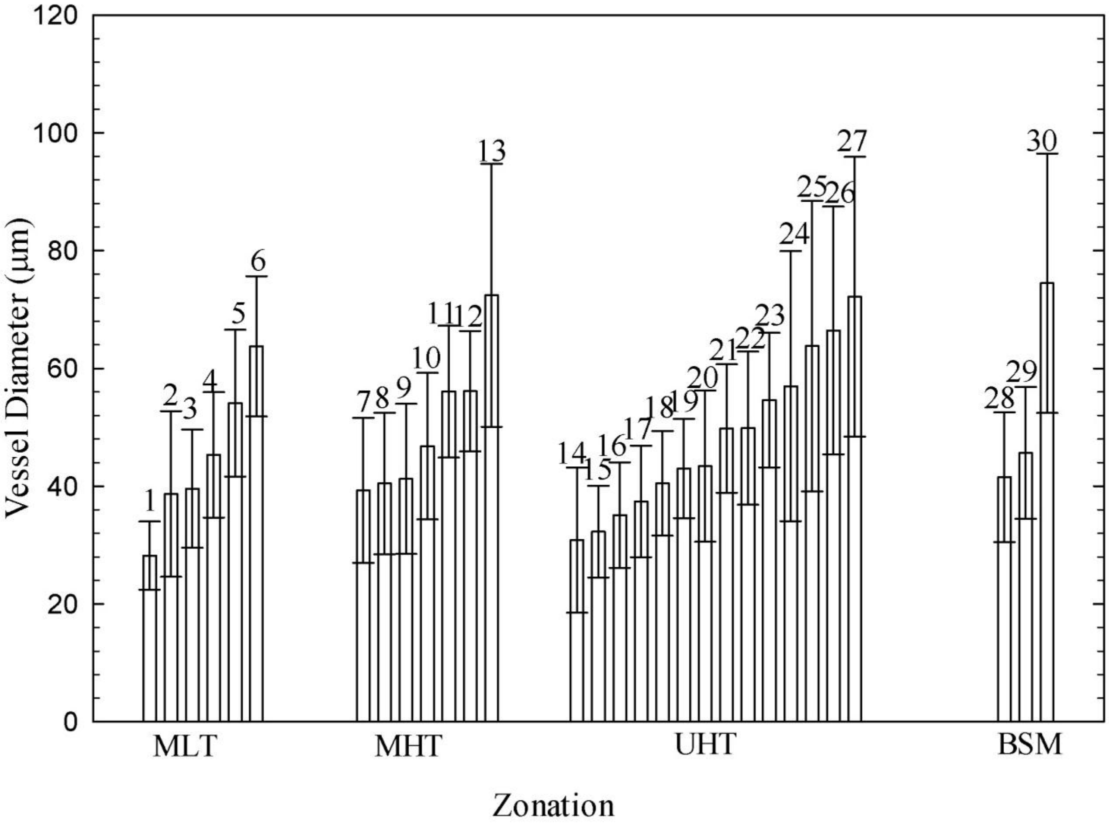

400
300
200
100
0
Vessel Density (number of vessels mm^{-2})
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Shrubs
Small-medium Trees
Large Trees
Growth forms

Figure 3.5.

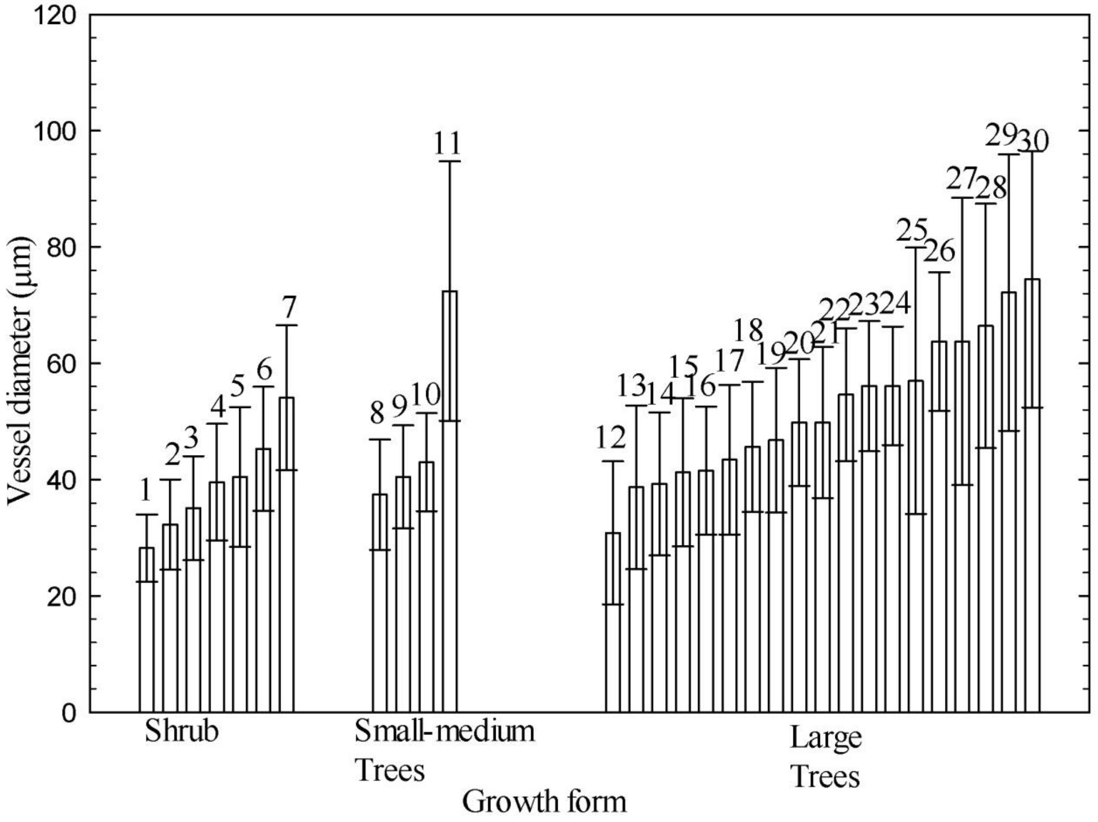
Figure 3.6. Variation in vessel diameter (d_V) among different zones in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1= *Aegiceras corniculatum*, 2 = *Avicennia marina*, 3 = *Aegilitis annulata*, 4 = *Osbornia octodonta*, 5 = *Pemphis acidula*, 6 = *Sonneratia alba*, 7 = *Xylocarpus australasicus*, 8 = *Acanthus ilicifolius*, 9 = *Brugueira gymnorrhiza*, 10 = *Rhizophora stylosa*, 11 = *Rhizophora mucronata*, 12 = *Rhizophora apiculata*, 13 = *Excoecaria agallocha*, 14 = *Avicennia alba*, 15 = *Luminitzera racemosa*, 16 = *Scyphiphora hydrophyllacea*, 17 = *Ceriops decandra*, 18 = *Ceriops tagal*, 19 = *Bruguiera exaristata*, 20 = *Xylocarpus rumphii*, 21 = *Bruguiera sexangula*, 22 = *Xylocarpus granatum*, 23 = *Bruguiera parviflora* 24 = *Avicennia officinalis*, 25 = *Heritiera littoralis*, 26 = *Myristica hollrungii*, 27 = *Dolichandrone spathacea*, 28 = *Stemonurus apicalis*, 29 = *Brugueira cylindrica*, 30 = *Cynometra ramiflora.*



Vessel Diameter (µm)
0
20
40
60
80
100
120
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
MLT
MHT
UHT
BSM
Zonation

Figure 3.6.

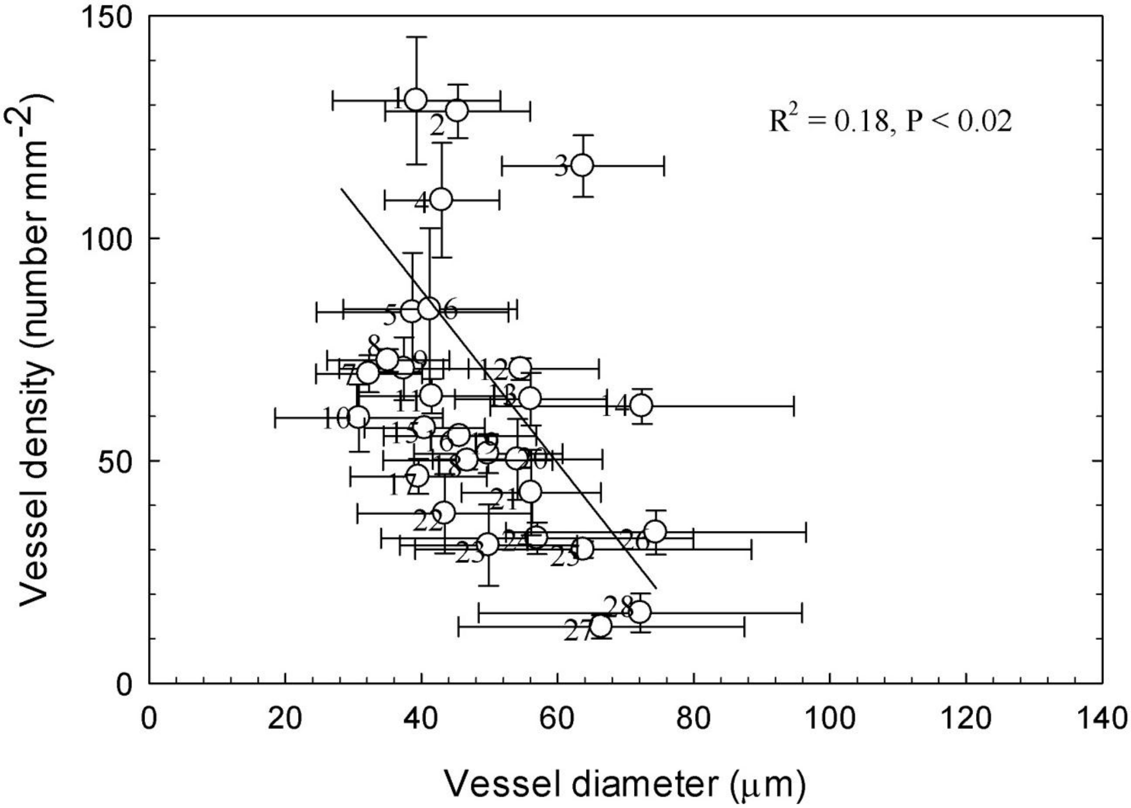
Figure 3.7. Variation in vessel diameter (d_V) among different growth forms in 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Aegiceras corniculatum*, 2 = *Luminitzera racemosa*, 3 = *Scyphiphora hydrophyllacea,* 4 = *Aegilitis annulata*, 5 = *Acanthus ilicifolius*, 6 = *Osbornia octodonta*, 7 = *Pemphis acidula*, 8 = *Ceriops decandra*, 10 = *Ceriops tagal*, 11 = *Brugueira exaristata*, 12 = *Excoecaria agallocha*, 12 = *Avicennia alba*, 13 = *Avicennia marina*, 14 = *Xylocarpus australasicus*, 15 = *Brugueira gymnorrhiza*, 16 = *Stemonurus apicalis*, 17 = *Xylocarpus rumphii*, 18 = *Bruguiera cylindrica*, 19 = *Rhizophora stylosa*, 20 = *Bruguiera sexangula*, 21 = *Xylocarpus granatum*, 22 = *Bruguiera parviflora*, 23 = *Rhizophora mucronata*, 24 = *Rhizophora apiculata*, 25 = *Avicennia officinalis*, 26 = *Sonneratia alba*, 27 = *Heritiera littoralis*, 28 = *Myristica hollrungi*, 29 = *Dolichandrone spathacea*, 30 = *Cynometra ramiflora.*



120
100
80
60
40
20
0
Vessel diameter (µm)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Shrub
Small-medium Trees
Large Trees
Growth form

Figure 3.7.

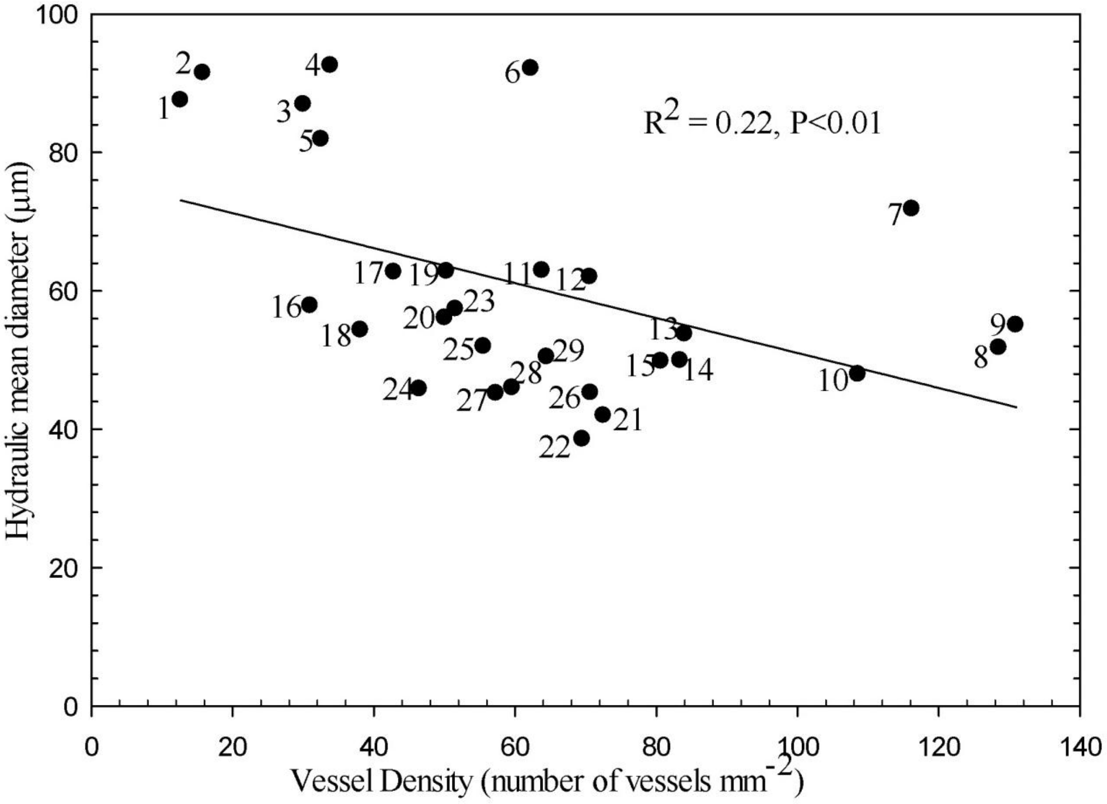
Figure 3.8. Correlation between vessel density and vessel diameter from 30 species of New Guinea mangroves. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Xylocarpus australasicus*, 2 = *Osbornia octodonta*, 3 = *Sonneratia alba*, 4 = *Brugueira exaristata*, 5 = *Avicennia marina*, 6 = *Brugueira gymnorrhiza*, 7 = *Brugueira cylindrica*, 8 = *Avicennia alba*, 9 = *Avicennia officinalis*, 10 = *Bruguiera parviflora*, 11 = *Bruguiera sexangula*, 12 = *Ceriops decandra*, 13 = *Ceriops tagal*, 14 =.*Acanthus ilicifolius*, 15 =.*Xylocarpus rumphii*, 16 = *Excoecaria agallocha*, 17 = *Stemonurus apicalis*, 18 = *Luminitzera racemosa*, 19 = *Xylocarpus granatum*, 20 = *Osbornia octodonta*, 21 = *Pemphis acidula*, 22 = *Rhizophora apiculata*, 23 = *Rhizophora mucronata*, 24 = *Rhizophora stylosa*, 25 = *Scyphiphora hydrophyllacea*, 26 = *Aegilitis annulata*, 27 = *Heritiera littoralis*, 28 = *Cynometra ramiflora*, 29 = *Myristica hollrungi*, 30 = *Dolichandrone spathacea*. Correlation coefficiency test showed $R^2 = 0.18$, $P < 0.02$ indicative of a strong relationship between vessel density (V_d) and vessel diameter (d_V).



Vessel density (number mm^{-2})
Vessel diameter (μm)
$R^2 = 0.18, P < 0.02$
0
20
40
60
80
100
120
140
0
50
100
150
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28

Figure 3.8.

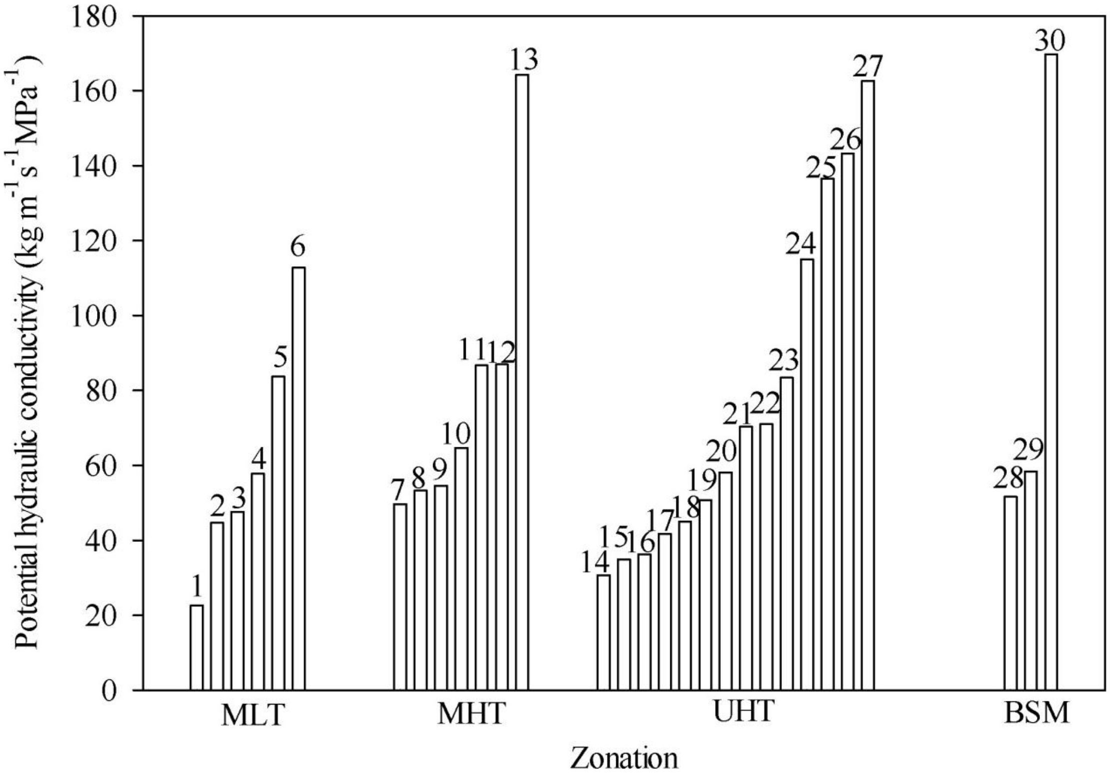
Figure 3.9. Relationship between mean vessel hydraulic diameter and vessel density of 29 mangrove species from New Guinea. Data points are means of 10 samples with error bars denoting the standard deviation around the mean. The numbers next to each bar refer to species listed as follows: 1 = *Myristica hollrungi*, 2 = *Dolichandrone spathacea*, 3 = *Heritiera littoralis*, 4 = *Cynometra ramiflora*, 5 = *Avicennia officinalis*, 6 = *Excoecaria agallocha*, 7 = *Sonneratia alba*, 8 = *Osbornia octodonta*, 9 = *Xylocarpus australasicus*, 10 = *Brugueira exaristata*, 11 = *Rhizophora mucronata*, 12 = *Bruguiera parviflora*, 13 = *Brugueira gymnorrhiza*, 14 = *Acanthus ilicifolius*, 15 = *Avicennia marina*, 16 = *Xylocarpus granatum*, 17 =*Ceriops tagal*, 18 = *Xylocarpus rumphii*, 19 = *Bruguiera sexangula*, 20 = *Pemphis acidula*, 21 = *Scyphiphora hydrophyllacea*, 22 = *Luminitzera racemosa*, 23 = *Rhizophora stylosa*, 24 = *Aegialitis annulata*, 25 = *Brugueira cylindrica*, 26 = *Ceriops decandra*, 27 = *Avicennia alba*, 28 = *Rhizophora apiculata*, 29 = *Stemonurus apicalis*. Regression analysis showed $R^2 = 0.22$, $P < 0.01$ indicative of a strong relationship between vessel density (V_d) and hydraulic mean diameter (d_h).



Hydraulic mean diameter (μm)
Vessel Density (number of vessels mm^{-2})
R^2 = 0.22, P<0.01
0
20
40
60
80
100
0
20
40
60
80
100
120
140
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

Figure 3.9.

Figure 3.11. Variation in potential hydraulic conductivity (kg m^{-2} s^{-1} MPa^{-1}) of 29 species of New Guinea mangroves among different zones. The numbers on the cap of each bar refer to species listed as follows: 1 = *Aegiceras corniculatum*, 2 = *Aegilitis annulata*, 3 = *Avicennia marina*, 4 = *Osbornia octodonta*, 5 = *Pemphis acidula*, 6 = *Sonneratia alba*, 7 = *Acanthus ilicifolius*, 8 = *Xylocarpus australasicus*, 9 = *Brugueira gymnorrhiza*, 10 = *Rhizophora stylosa*, 11 = *Rhizophora apiculata*, 12 = *Rhizophora mucronata*, 13 = *Excoecaria agallocha*, 14 = *Luminitzera racemosa*, 15 = *Avicennia alba*, 16 = *Scyphiphora hydrophyllacea*, 17 = *Ceriops decandra*, 18 = *Ceriops tagal*, 19 = *Bruguiera exaristata*, 20 = *Xylocarpus rumphii*, 21 = *Bruguiera sexangula*, 22 = *Xylocarpus granatum*, 23 = *Bruguiera parviflora*, 24 = *Avicennia officinalis*, 25 = *Heritiera littoralis*, 26 = *Myristica hollrungii*, 27 = *Dolichandrone spathacea*, 28 = *Stemonurus apicalis*, 29 = *Brugueira cylindrica,30 = Cynometra ramiflora*.



Potential hydraulic conductivity ($kg\ m^{-1}\ s^{-1}\ MPa^{-1}$)
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
MLT
MHT
UHT
BSM
Zonation

Figure 3.11.

Figure 3.12. Variation in potential hydraulic conductivity (kg m^{-2} s^{-1} MPa^{-1}) of 30 New Guinea mangrove species among different growth forms. The numbers on the cap of each bar refer to species listed as follows: 1 = *Aegiceras corniculatum*, 2 = *Luminitzera racemosa*, 3 = *Scyphiphora hydrophyllacea*, 4 = *Aegilitis annulata*, 5 = *Acanthus ilicifolius*, 6 = *Osbornia octodonta*, 7 = *Pemphis acidula,* 8 = *Cceriops decandra*, 9 = *Ceriops tagal*, 10 = *Brugueira exaristata*, 11 = *Excoecaria agallocha*, 12= *Avicennia alba*, 13 = *Avicennia marina*, 14 = *Stemonurus apicalis*, 15 = *Xylocarpus australasicus*, 16 = *Brugueira gymnorrhiza*, 17 = Xylocarpus rumphii, 18 = *Brugueira cylindrica*, 19 = *Rhizophora stylosa*, 20 = *Bruguiera sexangula*, 21 = *Xylocarpus granatum*, 22 = *Bruguiera parviflora*, 23 = *Rhizophora apiculata*, 24 = *Rhizophora mucronata*, 25 = *Sonneratia alba*, 26 = *Avicennia officinalis*, 27 = *Heritiera littoralis*, 28 = *Myristica hollrungi*, 29 = *Dolichandrone spathacea*, 30 = *Cynometra ramiflora.*

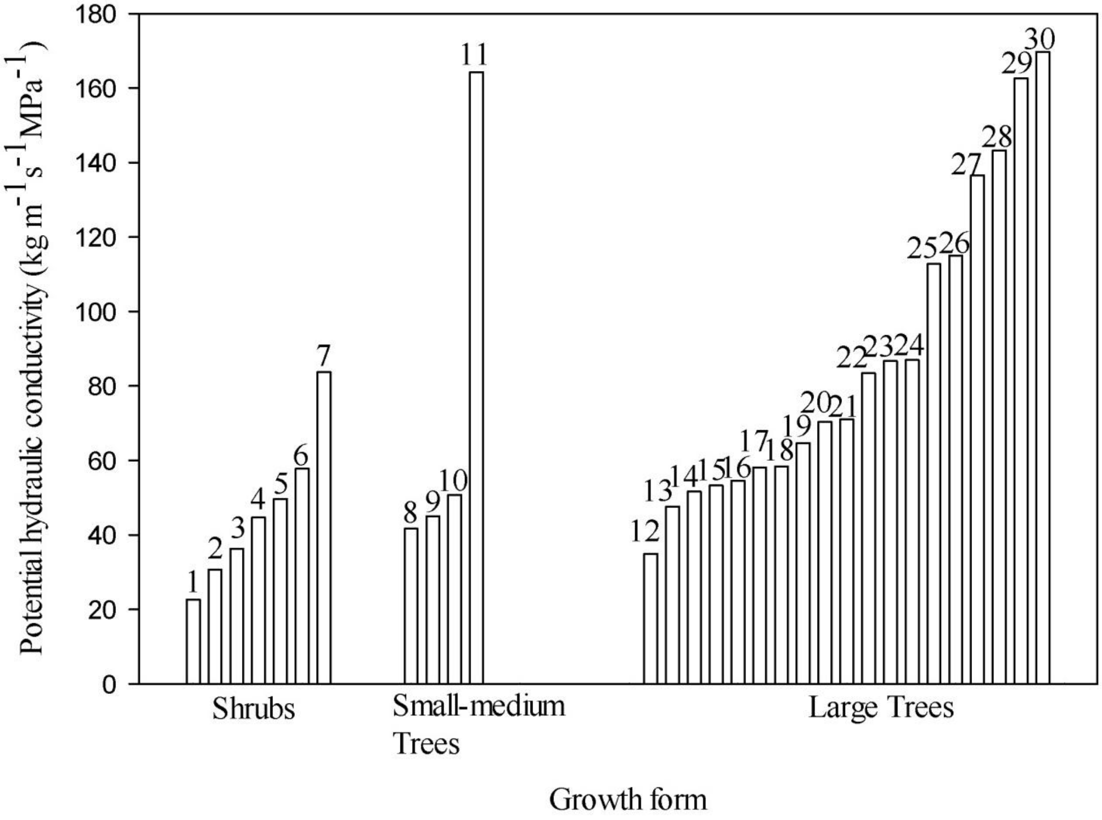

Potential hydraulic conductivity (kg m^{-1} s^{-1} MPa^{-1})
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Shrubs
Small-medium Trees
Large Trees
Growth form

Figure 3.12.

Figure 3.13. Relation of calculated potential hydraulic conductivity (K_p) with vein density (D_V) of 30 species of New Guinea mangroves. Data points are means of 10 samples and the numbers next to each symbols refer to species listed as follows: 1 = *Acanthus ilicifolius*, 2 = *Stemonurus apicalis*, 3 = *Ceriops decandra*, 4 = *Rhizophora mucronata*, 5 = *Ceriops tagal*, 6 = *Avicennia marina*, 7 = *Bruguiera sexangula*, 8 = *Pemphis acidula*, 9 = *Brugueira cylindrica*, 10 = *Bruguiera parviflora*, 11 = *Brugueira gymnorrhiza*, 12 = *Luminitzera racemosa*, 13 = *Heritiera littoralis*, 14 = *Rhizophora apiculata*, 15 = *Scyphiphora hydrophyllacea*, 16 = *Brugueira exaristata*, 17 = 18 = *Rhizophora stylosa*, 19 = Avicennia alba, 20 = Sonneratia alba, 21 = *Xylocarpus granatum*, 22 = *Aegilitis annulata*, 23 = *Xylocarpus rumphii*, 24 = *Osbornia octodonta*, 25 = *Xylocarpus australasicus*, 26 = *Avicennia officinalis*, 27 = *Myristica hollrungi*, 28 = *Dolichandrone spathacea*, 29 = *Cynometra ramiflora*, and 30 = *Excoecaria agallocha*. Regression analysis showed $R^2 = 0.0005$, $P > 0.05$ indicative of no relationship between vein density (D_V) and potential hydraulic conductivity (K_p).

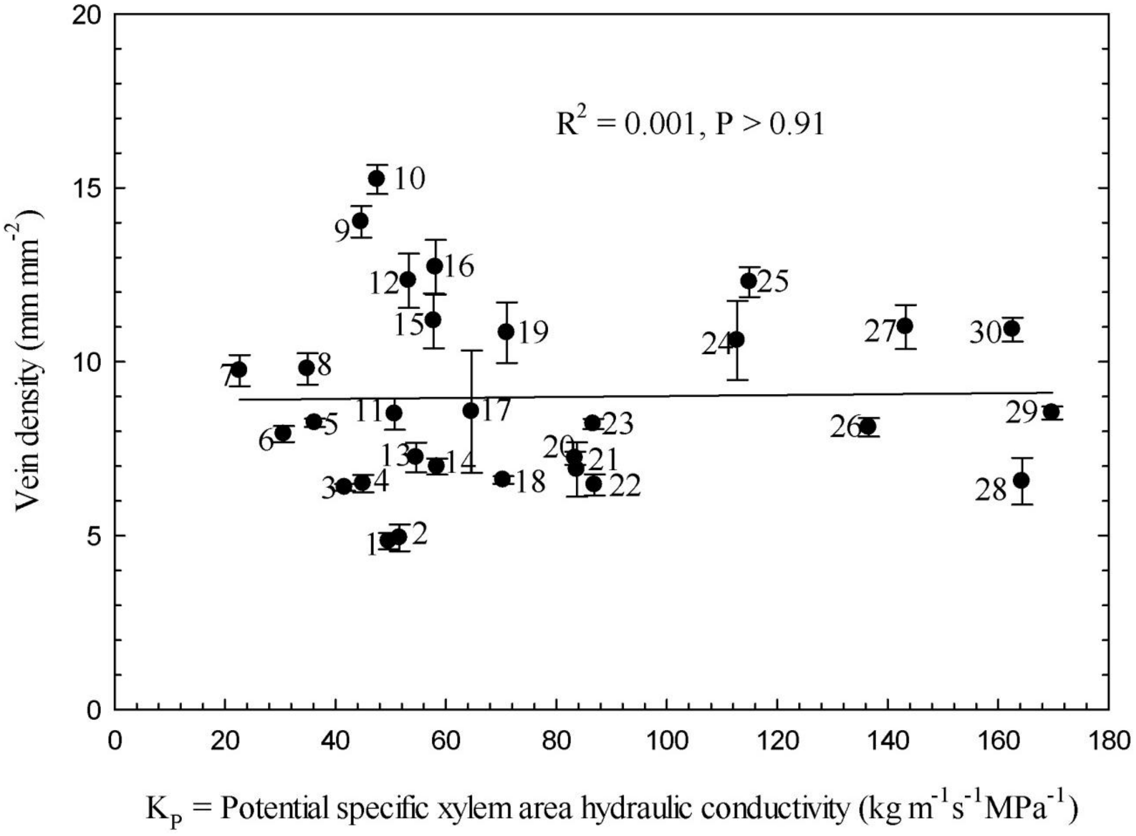
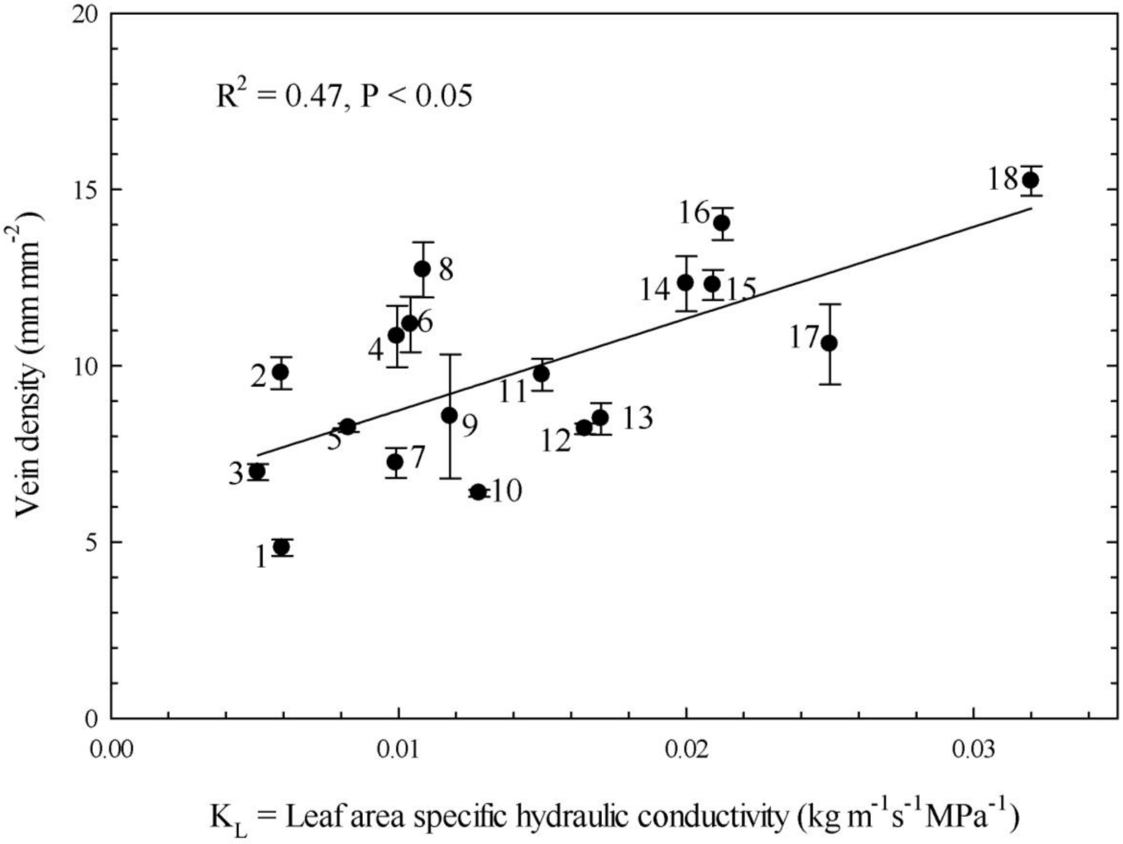

R² = 0.001, P > 0.91
Vein density (mm mm⁻²)
Kₚ = Potential specific xylem area hydraulic conductivity (kg m⁻¹s⁻¹MPa⁻¹)
0
5
10
15
20
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Figure 3.13

Figure 3.14. Relationship of calculated specific leaf area conductivity (K_L) with vein density (D_V). Data points are means of 10 samples and the numbers next to each symbol refer to species listed as follows: 1 = *Acanthus ilicifolius*, 2 = *Aegiceras corniculatum*, 3 = *Aegilitis annulata*, 4 = *Avicennia alba*, 5 = *Avicennia marina*, 6 = *Avicennia officinalis*, 7 = *Brugueira cylindrica*, 8 = *Brugueira exaristata*, 9 = *Brugueira gymnorrhiza*, 10 = *Ceriops decandra*, 11 = *Osbornia octodonta*, 12 = *Rhizophora apiculata*, 13 = *Rhizophora stylosa*, 14 = *Scyphiphora hydrophyllacea*, 15 = *Sonneratia alba*, 16 = *Xylocarpus australasicus*, 17 = *Xylocarpus granatum*, 18 = *Xylocarpus rumphii.* Regression analysis showed $R^2 = 0.47$, $P < 0.05$ indicative of a strong positive influence of vessel density (V_d) on specific leaf area conductivity (K_L).



R² = 0.47, P < 0.05
Vein density (mm mm⁻²)
K_L = Leaf area specific hydraulic conductivity (kg m⁻¹s⁻¹MPa⁻¹)
0
5
10
15
20
0.00
0.01
0.02
0.03
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Figure 3.14.

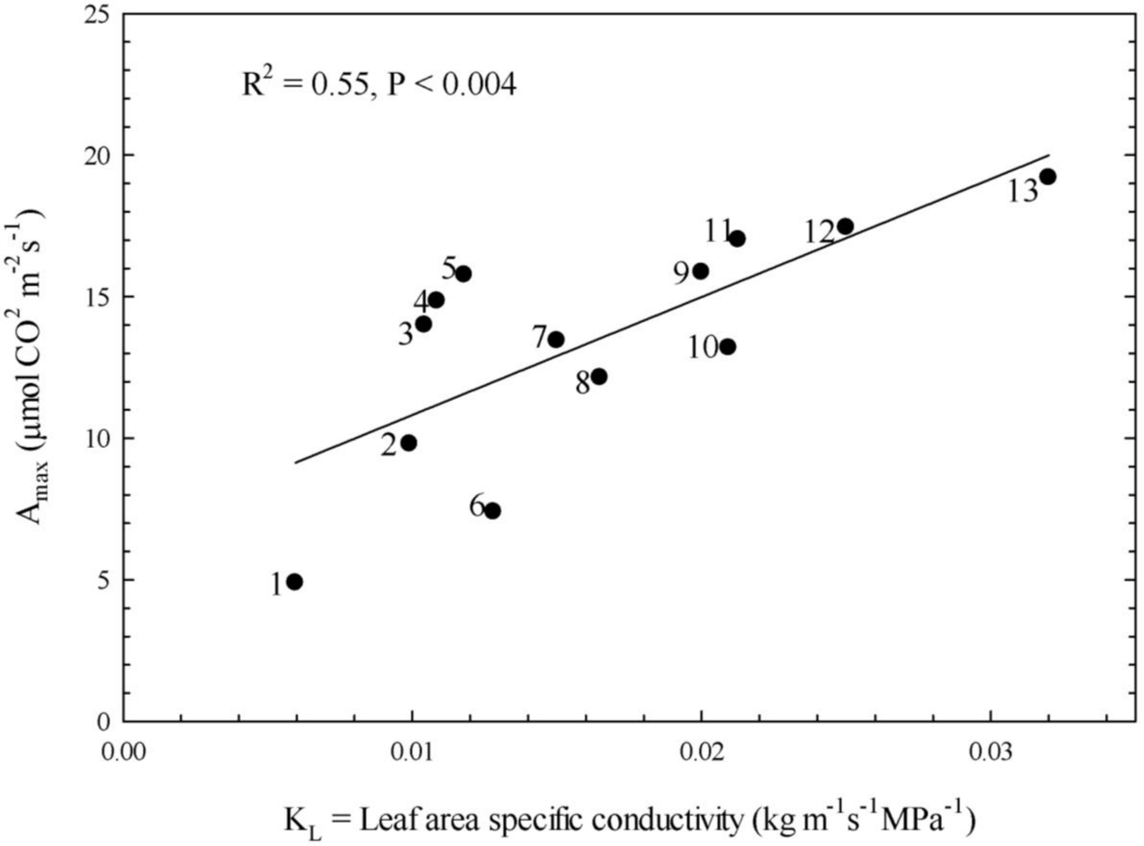


Figure 3.15. Correlation between calculated specific leaf area conductivity (K_L) with maximum photosynthetic carbon assimilation rate (A_{max}). Data points are means of 10 samples and the numbers next to each symbol refer to species listed as follows: 1 = *Acanthus ilicifolius*, 2 = *Ceriops decandra*, 3 = *Brugueira gymnorrhiza*, 4 = *Rhizophora apiculata*, 5 = *Rhizophora stylosa*, 6 = *Aegiceras corniculatum*, 7 = *Sonneratia alba*, 8 = *Osbornia octodonta*, 9 = *Avicennia officinalis*, 10 = *Xylocarpus australasicus*, 11 = *Xylocarpus rumphii*, 12 = *Aegilitis annulata*, 13 = *Avicennia marina.* Correlation coefficient showed $R^2 = 0.55$, $P < 0.05$ indicative of a strong positive correlation between leaf area conductivity (K_L) and photosynthetic carbon assimilation (A_{max}).

Figure 3.16. Correlation between calculated potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) and vessel density (D_V, number of vessels mm^{-2}). The data points are means of 10 samples and the number next to each symbol refer to species listed as follows; *1 =Luminitzera racemosa*, 2 = *Aegiceras corniculatum*, 3 = *Scyphiphora hydrophyllacea*, 4 = *Ceriops decandra*, 5 = *Avicennia alba*, 6 = *Ceriops tagal*, 7 = *Avicennia marina*, 8 = *Acanthus ilicifolius*, 9 = *Brugueira exaristata*, 10 = *Osbornia octodonta*,11 = *Xylocarpus australasicus*, 12 = *Brugueira gymnorrhiza*, 13 = *Stemonurus apicalis*, 14 = *Xylocarpus rumphii*, 15 = *Brugueira cylindrica*, 16 = *Rhizophora stylosa*, 17 = *Bruguiera sexangula*, 18 = *Xylocarpus granatum*, 19 = *Bruguiera parviflora*, 20 = *Aegialitis annulata*, 21 = *Pemphis acidula*, 22 = *Rhizophora apiculata*, 23 = *Rhizophora mucronata*, 24 = *Sonneratia alba*, 25 = *Avicennia officinalis*, 26 = *Heritiera littoralis*, 27 = *Myristica hollrungii*, 28 = *Dolichandrone spathacea*, 29 = *Excoecaria agallocha*, 30 = *Cynometra ramiflora.* Correlation coefficient showed $R^2 = 0.21$, $P < 0.01$ indicative of a strong inverse correlation between potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) and vessel density (number of vessel mm^{-2}).

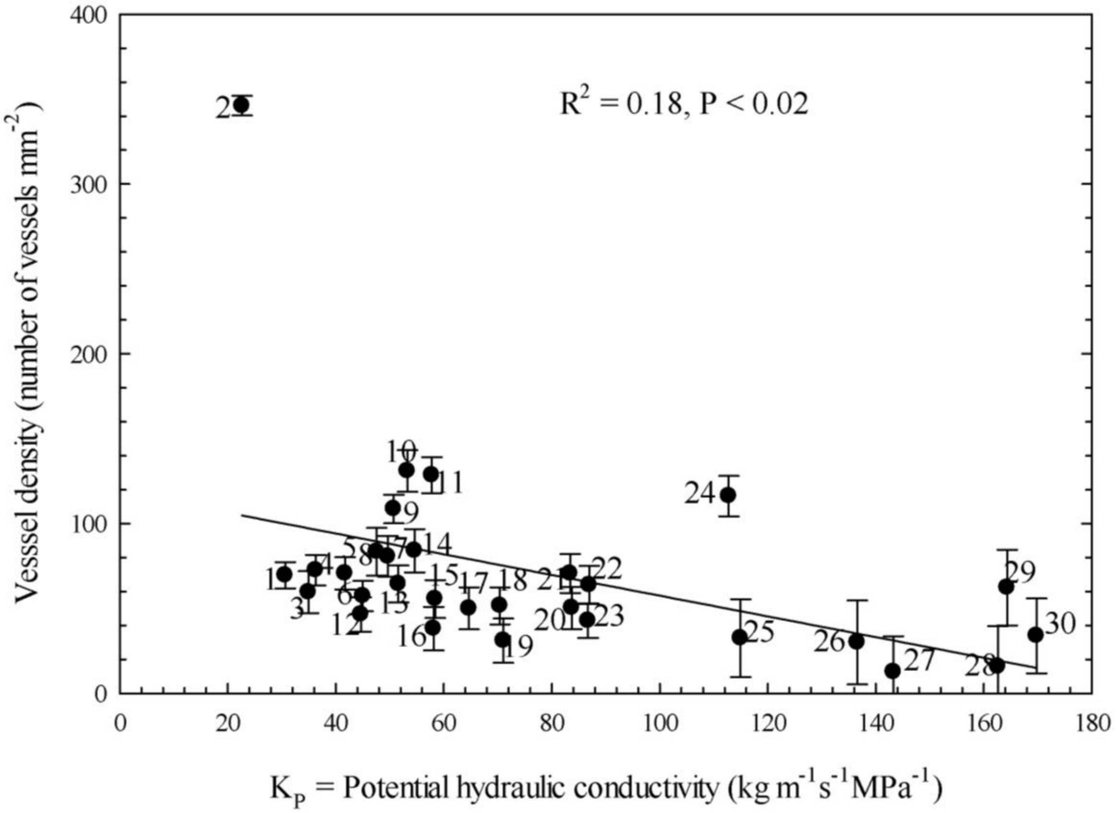
R^2 = 0.18, P < 0.02
Vessel density (number of vessels mm^{-2})
K_P = Potential hydraulic conductivity (kg m^{-1}s^{-1}MPa^{-1})
0
100
200
300
400
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Figure 3.16.

Figure 3.17. Correlation between calculated potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) and vessel diameter (d_V, µm). The data points are means of 10 samples and the number next to each symbol refer to species listed as follows; 1 = *Aegiceras corniculatum*, 2 = *Luminitzera racemosa,* 3 = *Avicennia alba,* 4 = *Scyphiphora hydrophyllacea*, 5 = *Ceriops decandra*, 6 = *Aegilitis annulata*, 7 = *Ceriops tagal*, 8 = *Avicennia marina*, 9 = *Acanthus ilicifolius*, 10 = *Brugueira exaristata*, 11 = *Stemonurus apicalis*, 12 = *Xylocarpus australasicus*, 13 = *Brugueira gymnorrhiza*, 14 = *Osbornia octodonta*, 15 = *Dolichandrone spathacea*, 16 = *Brugueira cylindrica*, 17 = *Rhizophora stylosa*, 18 = *Bruguiera sexangula*, 19 = *Xylocarpus granatum*, 20 = *Bruguiera parviflora*, 21 = *Pemphis acidula*, 22 = *Rhizophora apiculata*, 23 = *Rhizophora mucronata*, 24 = *Sonneratia alba*, 25 = *Avicennia officinalis*, 26 = *Heritiera littoralis*, 27 = *Myristica hollrungi*, 28 = *Dolichandrone spathacea*, 29 = *Excoecaria agallocha*, 30 = *Cynometra ramiflora*. Correlation coefficient showed $R^2 = 0.95$, $P < 0.0001$ indicative of a very strong positive correlation between potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) and vessel diameter (µm).

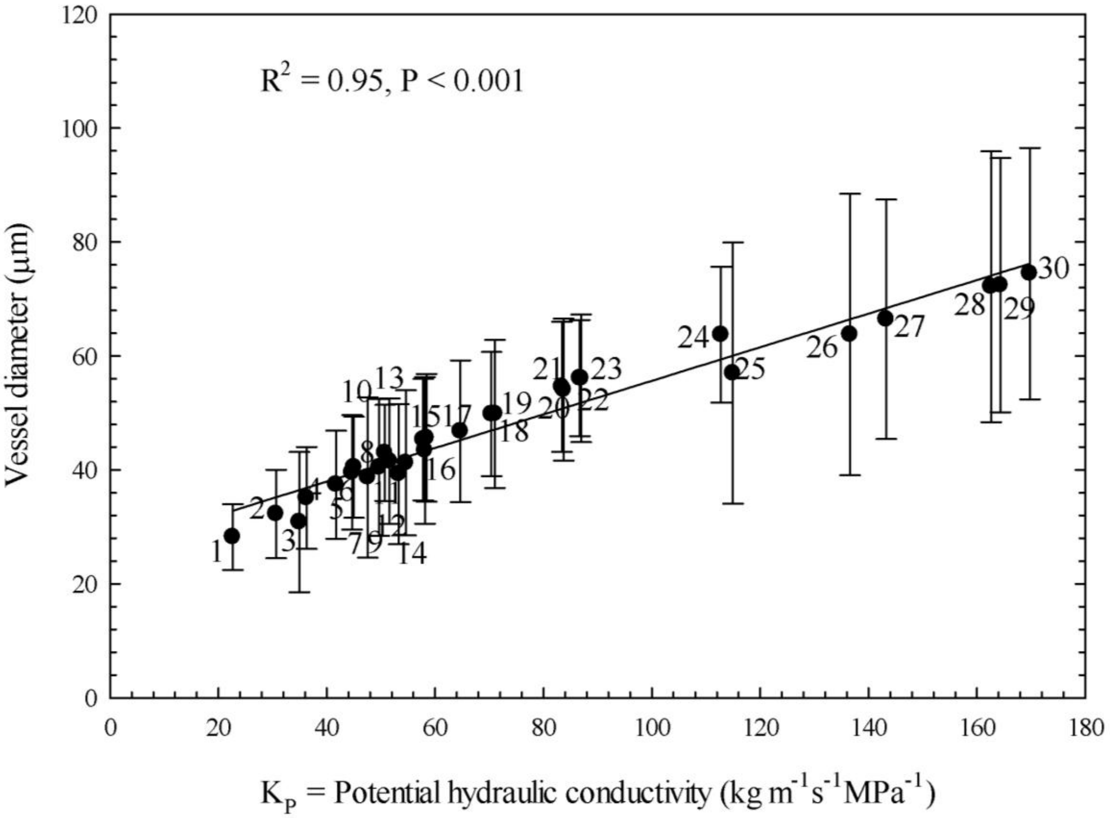
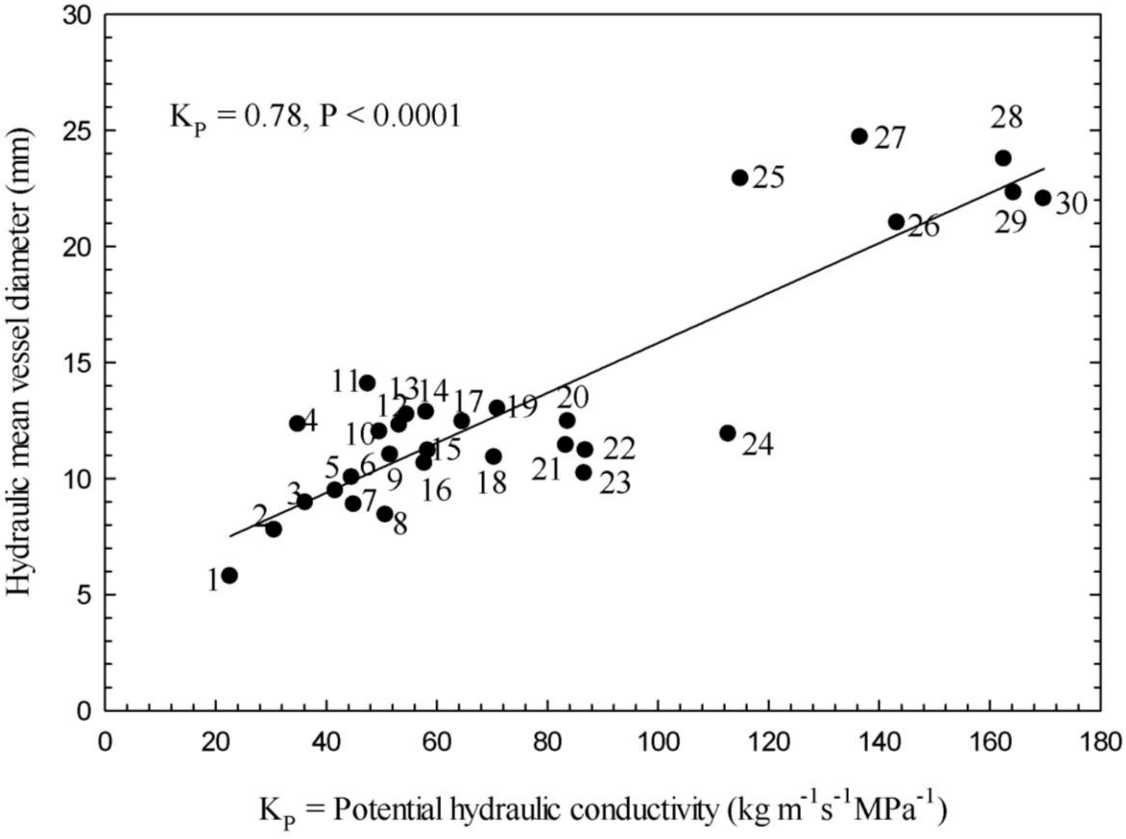

R² = 0.95, P < 0.001
Vessel diameter (μm)
K_P = Potential hydraulic conductivity (kg m⁻¹s⁻¹MPa⁻¹)
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Figure 3.17.

Figure 3.18. Correlation between calculated potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) and mean hydraulic vessel diameter (d_h, µm). The data points are means of 10 samples and the number next to each symbol refer to species listed as follows; 1 = *Aegiceras corniculatum*, 2 = *Luminitzera racemosa*, 3 = *Avicennia alba*, 4 = *Scyphiphora hydrophyllacea*, 5 = *Aegilitis annulata*, 6 = *Ceriops tagal*, 7 = *Bruguieria sexangula*, 8 = *Pemphis acidula*, 9 = *Brugueira cylindrica*, 10 = *Bruguiera parviflora*, 11 = *Bruguiera gymnorrhiza*, 12 = *Stemonurus apicalis*, 13 = *Osbornia octodonta*, 14 = *Rhizophora apiculata*, 15 = *Rhizophora mucronata*, 16 = *Bruguiera exaristata*, 17 = *Avicennia marina*, 18 = *Rhizophora stylosa*, 19 = *Acanthus ilicifolius*, 20 = *Ceriops decandra*, 21 = *Sonneratia alba*, 22 = *Xylocarpus granatum*, 23 = *Xylocarpus rumphii*, 24 = *Xylocarpus australasicus*, 25 = *Avicennia officinalis*, 26 = *Heritiera littoralis*, 27 = *Myristica hollrungii*, 28 = *Dolichandrone spathacea*, 29 = *Excoecaria agallocha*, 30 = *Cynometra ramiflora*. Correlation coefficient showed $R^2 = 0.78$, $P < 0.0001$ indicative of a very strong positive correlation between potential hydraulic conductivity (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) and mean hydraulic vessel diameter (µm).



$K_P = 0.78$, $P < 0.0001$
Hydraulic mean vessel diameter (mm)
K_P = Potential hydraulic conductivity (kg $m^{-1}s^{-1}MPa^{-1}$)
0
5
10
15
20
25
30
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
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29
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Figure 3.18.

Figure 3.19. Five predominant rooting system type (RST) found in the coexisting mangrove species. The assigned zone is where the RST is predominant. The mean of wood functional traits; wood density (P_{wood}), vessel density (V_d), vessel diameter (d_V), and hydraulic mean diameter (d_h) for species with different RST is provided.

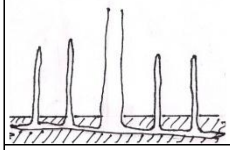
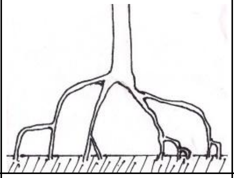
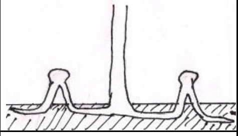
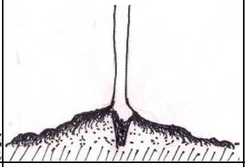
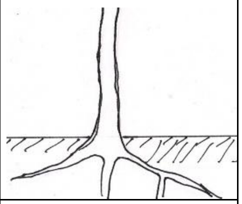
P_{wood} = 0.76 ± 0.04 g m^{-2}	P_{wood} = 0.61 ± 0.04 g m^{-2}	P_{wood} = 0.70 ± 0.04 g m^{-2}	P_{wood} = 0.70 ± 0.04 g m^{-2}	P_{wood} = 0.70 ± 0.04 g m^{-2}
V_d = 67.64 ± 7.06 number vessels mm^{-2}	V_d = 46.78 ± 4.80 number vessels mm^{-2}	V_d = 71.19 ± 6.60 number vessels mm^{-2}	V_d = 57.52 ± 8.54 number vessels mm^{-2}	V_d = 95.50 ± 5.15 number vessels mm^{-2}
d_V = 45.96 ± 14.25 µm	d_V = 53.39 ± 13.17 µm	d_V = 44.59 ± 10.43 µm	d_V = 49.08 ± 15.71 µm	d_V = 50.50 ± 13.97 µm
d_h = 14.25 ± 5.05	d_h = 13.17 ± 4.46	d_h = 10.43 ± 1.56	d_h = 15.71 ± 6.00	d_h = 13.97 ± 6.88
				
Pneumatophore RST	Prop/Stilt RST	Knee-like RST	Plank buttressed RST	Unbuttressed RST
MLT Zone	MLT-MHT Zone	MHT-UHT Zone	UHT-BSM Zone	BSMZone

Figure 3.19.

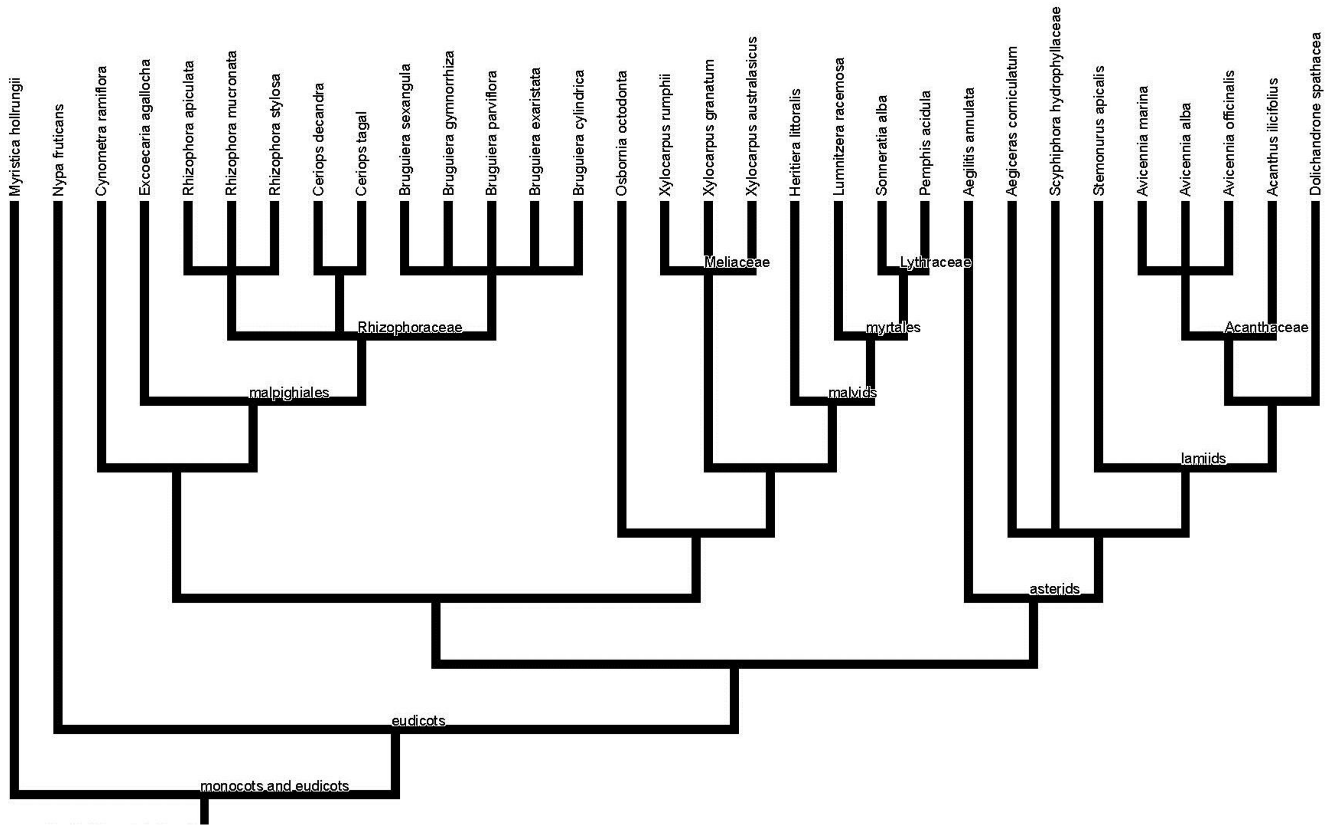


Figure 3.21. Phylogenetic tree of 31 mangrove species from New Guinea built on a phylogeny tree backbone from the R20100701 tree from Phylomatic; downloaded on March 2010 from the APG3 derived megatree (Webb *et al.* 2007). Family level relationship was constructed on R20100701 tree backbone based on Stevens 2001.

DISCUSSION

Wood functional traits such as wood density, vessel hydraulic mean diameter, and vessel density significantly influence the stability, carbon gain, growth and survival of plants (Baas 1987, Sperry *et al*. 2008, Poorter *et al*. 2010). Wood traits are of key importance because they reflect the long term investment strategy of a plant, and because wood is so expensive to construct and has low turn over rates; it provides good information on the long term ecological implications of a species.

The present study revealed that coexisting mangrove species differed considerably in wood (P_{wood}, V_d, d_V) and hydraulic (K_P, K_L) functional traits among different zones, plant growth forms, and root system types (RST). P_{wood} correlated with leaf mass per area (LMA); a resource use strategy trait. The stem hydraulic functional traits (K_P and K_L) correlated with a suite of leaf functional traits; D_V, LMA, A_{max}, and g_{smax}. The detection of good relations is very remarkable because there were wide differences in stress level and growth forms that were measured. In the following discussion, I discuss the specific relations between the different functional traits, zonation, root system types, and growth forms.

Relationship between Wood density, Zonation, and Growth forms

Wood traits (P_{wood}, d_V, V_d, d_h) and stem hydraulic traits (K_P, K_L, H_V) provide information on trees' different strategies in response to multiple demands for optimal hydraulic conductivity, safety (Vernheyden *et al*. 2005, Robert *et al.* 2009, Zhang *et al*. 2009), and their subsequent influence on photosynthesis, productivity, growth, and survival (Brodribb *et al*. 2007, Feild and Balun 2007, Hudson *et al*. 2010). Previous investigations on relations in hydraulic functional traits and photosynthetic gas exchange properties of mangrove species showed strong linkages between hydraulic traits and photosynthetic gas exchange processes (Sobrado 1999, Vernheyden *et al*. 2005, Lovelock *et al.* 2006, 2010, Robert *et al.* 2009, Zhang *et al*. 2009). There are, however, no data on relations between wood traits and biogeochemical environmental gradient (zonation) and growth form regarding mangroves. Previous studies incorporated only a few selected taxa; therefore, inferences to hyperdiverse mangrove communities such as those in New Guinea (Giensen *et al*. 2007) are questionable.

A current, widely held paradigm on functional diversity and performance of mangrove ecosystems is that mangroves despite being abundantly immersed in water have high water constraint and therefore have a conservative water use strategy *sensu* (Ball and Farquhar 1984, Ball *et al*. 1988, Feller 1995, Sobrado 2001, Feller *et al*. 2003, Lovelock *et al*. 2006, Martin *et al*. 2010). In contrast to my hypothesis, I found marked variation in the wood and hydraulic functional performance of species across zonation and between growth forms. My results suggest that mangroves despite occupying a narrow habitat range and pronounced morphological convergence have evolved functional and structural traits that enable functional diversity in performance.

My results indicate significant differences in P_{wood} among different zones (Fig. 3.0, 3.1, Table 3.1) suggesting that the observed differences in the P_{wood} are linked to the local biogeochemical gradient (zonation). The highest mean P_{wood} (0.73 ± 0.03 g m^{-3}) was observed in *Pemphis* in the MLT zone, followed by the MHT zone (0.70± 0.02 g m^{-3}), the UHT zone (0.68± 0.02 g m^{-3}), and the lowest in the BSM zone (0.64± 0.03 g m^{-3}). The duration of tides':- mean low tide (MLT), medium high tide (MHT), upper high tide (UHT), and Spring tide in the back swamp mangrove (BSM) varied persistently throughout the year, and the four different zones observed in my study reflect different tide durations. The longest tide duration was observed in the mean MLT and declined in the landward direction. Zones with the longest tide duration had the highest salinity exposure and vise-versa for zones with the shortest salinity exposure. My results indicate that xylem anatomy is moderated by biogeochemical factors, in particular tidal duration, which led to a coordinated increase in P_{wood} with increasing tidal duration. This explanation is consistent with previous studies' findings (Sobrado 1999, Verheyden *et al*. 2005, Sobrado 2006). In addition, my results indicated significant mean differences in P_{wood} between the following zones: MLT versus BSM, MHT versus BSM, UHT versus BSM (Table 3.0).

The P_{wood} in mangrove community is remarkably high in contrast to tropical and temperate forest communities. For example, mean P_{wood} from 17 dipterocarp species of 0.54 g m^{-3} (Zhang and Chao 2009), 0.58 g m^{-3} from 42 rainforest tree species (Poorter *et* *al*. 2010), and 0.54 g cm^{-3} from 30 temperate tree species (Aiba and Nakashizuka 2009) are all lower than mean of mangrove (0.68 g m^{-3}). This suggests that mangrove species are among the world most high density wood.

Previous studies on the relationship between wood traits and salinity showed that vessel density (V_d) increases with salinity while vessel diameter (d_V) and mean hydraulic diameter (d_h) decline (Sobrado 2006). Examination of wood anatomical traits (Fig.3.8, 3.16, Table 3.2) showed an inverse correlation between vessel density (V_d) and vessel diameter (d_V) (Fig.3.8) and between hydraulic mean diameter (d_h) and vessel density (V_d) (Fig.3.15). These relationships in vessel features indicate a trade-off between hydraulic efficiency (large d_V, low V_d, high d_h) and hydraulic safety (small d_V, high V_d, low d_h), which is consistent with earlier studies (Verheyden *et al*. 2005, Schmitz *et al*. 2006, Sobrado 2006, Sperry *et al.* 2008, Robert *et. al*. 2009, Poorter *et al.* 2010). The pattern observed in P_{wood} across zonation in my study is congruent with that of Sobrado (2006). I observed highest P_{wood} in the MLT zone, which is the most exposed zone to tidal and wind action, and lowest P_{wood} in the BSM zone (Table 3.1), which is more stable and least exposed to wave and wind action. It can be inferred that the species in the unstable zone (i.e. MLT) invest more heavily in hydraulic safety than efficiency. My results on the relationship between P_{wood} to zonation clearly show that mangroves have a much wider functional performance than the current widely held paradigm that considers mangroves as having narrow functional performance (Ball and Farquhar 1984, Ball *et al*. 1988, Ball 1996). Instead, my results provide the first evidence that a diverse range of xylem hydraulic strategies are occuring in the mangroves.

Examination of the relationship between P_{wood} (g cm^{-3}) and growth forms provided evidence for appreciable variation among different growth forms (Fig. 3.1, Table 3.1). P_{wood} varied among the shrubby growth forms, ranging from 0.56 ± 0.02 g m^{-3} in *Acanthus ilicifolius* to 0.94 ± 0.02 g m^{-3} *Pemphis acidula*, among small-medium trees, ranging from 0.55 ± 0.02 g m^{-3} in *Excoecaria agallocha* to 0.81 ± 0.04 g m^{-3} in *Bruguiera exaristata*, and among large trees, ranging from 0.35 ± 0.02 g m^{-3} *Dolichandrone spathacea* to 0.92 ± 0.02 g m^{-3} in *Rhizophora stylosa*. However, no differences in mean P_{wood} existed among the three different growth forms. In addition, no correlation existed between P_{wood} and plant growth forms.

Relationship between root system types and wood density

P_{wood} density varied significantly among different root system types (RSTs; Fig. 3.3, Table 3.0, 3.1). Pneumatophore RST exhibited the highest mean P_{wood} (0.76 ± 0.04 g m^{-3}), followed 'knee-like' RST (0.71 ± 0.03 g m^{-3}), plank buttressed (0.70 ± 0.04 g m^{-3}), unbuttressed RST (0.70 ± 0.04 g m^{-3}), and stilt/prop RST the lowest (0.69 ± 0.03 g m^{-3}). The universal trend in wood functional traits (P_{wood}, V_d, d_V, d_h) reflecting differential resource investment strategies is that increase in P_{wood} density is paralleled by increase in V_d, and decrease in d_V and d_h (Sperry *et al*. 2008, Poorter *et al*. 2010). My results on the wood functional traits among different RSTs (Table 3.1, 3.2, 3.3, 3.4, Fig. 3.19) do not conform to the above-described universal trend. Instead my results showed wood functional traits (P_{wood}, d_V, V_d, d_h) differed consistently among RSTs. For example, taxa with highest P_{wood} did not have the corresponding highest V_d, lowest d_V and d_h. Species with pneumatophore RST that had the highest P_{wood} had lower V_d than those with low P_{wood}, for example, unbuttressed RST and knee-like RST. Additionally, pneumatophore RST having the highest P_{wood}, intuitively should have the lowest d_h yet instead it had the highest. The wood functional traits measured from the previous studies are from land plants with potentially uniform RST. I speculate that the trend observed in my study is attributed to variation in the functional performance among different RSTs. I further speculate that P_{wood} functional traits in mangrove species are modulated by the rooting architecture. Apparently, the relationship between RST and P_{wood} has not been reported, and my observations are the first to describe the relationship. Species with pneumatophores (*Avicennia marina, Sonneratia alba*) were prominent in MLT zone. The relative high P_{wood} density in pneumatophore RST may reflect the salinity gradient, as pneumatophore RST are predominant in MLT zone and as such P_{wood} intuitively should be highest in the pneumatophore RSTs (Schmitz *et al*. 2006, Sobrado 2006). In contrast to the pneumatophore RST wood functional traits' relations, the stilt/prop RSTs that are also predominant in MLT zone had low P_{wood} and V_d, and high d_V and d_h. The unbuttressed RSTs in the BSM and UHT zones (which have the lowest salinity level) on the other hand showed higher P_{wood} density then those in the higher salinity zones. My results thus, reveal mangroves evolved distinctive specialization in wood traits toward multiple functions. Significant differences in mean P_{wood} were found among different root system types. Results showed that P_{wood} between stilt/prop RST versus unbuttressed RST, pneumatophore RST versus unbuttressed RST, knee-like RST versus unbuttressed

RST, and plank buttress RST versus unbuttressed RST all had significantly ($P < 0.001$) higher mean differences (Table 3.0).

A broad trend in wood functional traits is that when P_{wood} density increases, V_d increases. When V_d increases, d_V and d_h decrease (Aiba and Nakashizuka 2009, Zhang and Cao 2009). My results do not conform to this universal rule on wood functional trade-offs, instead my results showed that pneumatophore RST with the highest P_{wood} had lower V_d then unbuttressed RST. This indicates that other additional underlying mechanisms are involved in modulating the wood functional traits in the mangroves. Stilt/Prop root species have relatively low P_{wood} and have the lowest V_d and highest d_h, indicating a trade-off toward efficient hydraulic conductivity. Stilt/Prop RST species are in the most unstable zone and should be investing in mechanical stability but the data show that this is not the case. The stilt/prop RST species adapt to their environment through development of numerous propping stilt roots which contribute to substantial increase in whole plant mechanical support, therefore allow the species to specialize in other functions, in this case hydraulic efficiency.

A future study correlating P_{wood} and the biomechanical properties (Youngs' modulus Elasticity) of the different RSTs is important to ascertain the above speculations concerning the trade-off between growth and mechanical stability. Inclusion of biomechanical data will enable better understanding on relative investments in mechanical strength by different RSTs.

The relationship in the RST and P_{wood} observed in my study are consistent with the previous studies (Schmitz *et al*. 2006, Sperry *et al*. 2008, Robert *et al*. 2009, Poorter *et al*. 2010). The pneumatophore-bearing RSTs provide less resistance to vertical forces (wind, wave actions), therefore the pneumatophore-bearing RSTs species have high investment costs in mechanical support (i.e. low hydraulic efficiency in favor of high wood density). Stilt/Prop RSTs occupy similar zones as pneumatophore RSTs and should therefore have high P_{wood} and V_d. However, my results showed low P_{wood} and V_d in Stilt/Prop RSTs, a strategy benefiting hydraulic efficiency. It appears that the stilt root architecture is providing greater mechanical support to the axil (prmary) stem, which freed the wood to specialize in other functions, in this case an increased investment in hydraulic efficiency.

Relations between vessel density, zonation, and growth forms

The relationship between vessel diameter (d_V) and vessel density (V_d) traits reflect a trade-off between hydraulic efficiency and safety. The universal trend for vessel number per area decreases with increasing vessel diameter. When vessel diameter exceeds the theoretical packing limit, it compromises between maximizing area for conduction versus mechanical support and storage (Sperry *et al*. 2008). Second, the relationship between d_V and V_d traits may potentially reflect a trade-off between parenchyma and fibre tissues (i.e. storage and strength respectively) (Sperry *et al*. 2008, Robert *et al*. 2009, Poorter *et al*. 2010). Low P_{wood}, V_d and wide vessels are associated with fast growth and light demanding species. High P_{wood}, V_d and narrow vessels on the other hand are characteristics of slow growth and shade loving species (Poorter *et al.* 2010).

Examination of wood functional and vessel density traits (V_d, number of vessel mm^{-2}) from the 30 species from hyperdiverse mangrove communities in New Guinea varied among different zones and growth forms (Fig. 3.4, 3.12, Table 3.2). A PMC pos hoc test showed main difference was in V_d between MLT zone versus BSM zone and MLT zone versus UHT zone. V_d was highest at MLT zone and decreased in the landward direction. The mean V_d at MLT was 128.49 ± 3.91 SD number vessels mm^{-2} followed by MHT (73.51 ± 3.26 SD number vessels mm^{-2}), UHT (51.47 ± 2.47 SD number vessels mm^{-2}) and BSM (51.30.49 ± 3.46 SD number vessels mm^{-2}) zone, respectively (Fig. 3.4, 3.12). Maximum V_d (346.06 ± 6.46 number of vessel mm^{-2}) was recorded in *Aegiceras corniculatum*, and the minimum (12.66 ± 2.61 number of vessel mm^{-2}) was recorded in *Myristica hollrungii* (Fig.3.11).

The trend observed in which the V_d increased toward the seaward direction is consistent with previous glasshouse research (Verheyden *et al*. 2005, Schmitz *et al*. 2006, Sobrado 2006). These earlier glasshouse studies investigating the relationship between wood anatomy and salinity indicated that V_d increased with salinity. My results based on field observation provide a broader understanding on variation in wood anatomical traits in hyperdiverse mangrove communities. My results on V_d did not support my a priori hypothesis, in which I hypothesized that mangroves have narrow functional performance despite their wide phylogenetic affinities. Rather my data further demonstrate that mangrove communities exhibit a much wider functional performance.

V_d did not differ among different growth forms (Fig. 3.5, Table 3.2). Lack of significant differences in V_d among different growth forms observed in this study is consistent with those of earlier studies (Verheyden *et al*. 2005, Schmitz *et al*. 2006, Sobrado 2006, Poorter *et al.* 2010). These earlier studies pointed out that anatomical traits (V_d, d_V, d_h) are strongly linked to salinity, which is paralleled by biogeochemical environmental gradient persistent in the intertidal zones and not growth forms.

V_d correlates positively with salinity gradient (Verheyden *et al.* 2005, Schmitz *et al.* 2006, Sobrado 2006). In this study, salinity gradient can be equated to zonation, i.e. different zones noted in this study are demarcated by biogeochemical environmental gradients of which salinity is predominant. As such, d_V should be highest at the MLT zone and decrease in the landward direction. My results showed significant differences among different zones, which proximate salinity.

Besides salinity, other factors including phenology (Slim *et al.* 1996, Drew 1998, Choat *et al.* 2005, Coupland *et al.* 2005), nutrient availability (February and Manders 1999, Alongi *et al.* 2005), and water availability have been observed to influence d_V. Vessel density has been reported in previous studies to differ between xerophyte and mesophyte, the former had higher vessel density than the latter (Baas *et al.* 1983, Carlquist and Hoekman 1985, Lindorf 1994). Decrease in vessel density was also speculated to be linked to reduction in Auxin (a plant hormone responsible for cell elongation in meristems) because of salt stress interference on uptake of nutrients such as Ca^{2+}, Mg^{2+}, and K^+ (Popp *et al.* 1985, Aloni 2004, Súarez and Medina 2006). These studies indicated differences in wood functional traits (V_d, d_V, d_h) in mangroves can be modulated by salinity, temperature, hydroperiods, nutrient levels, and plant hormones. My study investigated variation among zonation, which is a good blanket proxy for salinity, hydroperiods, and nutrient levels.

High salinity is considered to create an osmotic stress, which increases risk of xylem vessel cavitation and subsequent embolism (Sperry and Tyree 1988, Hacke and Sperry 2001). The associated increase in d_V thus can be interpreted as a strategy for hydraulic safety. There are two possible benefits under the hydraulic safety strategy. First, when the same number of vessels is cavitated, a high percentage of transport system remains functional in wood of high d_V than in wood of low V_d (Bass *et al*. 1983, Villar-Salvador *et al*. 1997, Mauseth and Plemons-Rodriguez 1998). Second, because vessels are connected along their length via inter-vessel pits the embolized vessels can be circumvented by means of the large number of alternative routes for water transport (Tyree *et al*. 1994, Carlquist 2001). Besides an increase in V_d as a strategy for optimizing hydraulic safety, decrease in vessel diameter (d_V) has also been correlated to hydraulic safety as well (Arnold and Mauseth 1999, Stevenson and Mauseth 2004).

Relations between Vessel diameter, Zonation, and Growth forms

There were no significant differences in mean vessel diameter (d_V, µm) among different zones. (Fig. 3.6). However, there was significant difference in d_V among different growth forms (shrub, small-medium tree, large tree) (Fig. 3.7). The trends observed in the relationship between vessel diameter (d_V), growth forms and zonation suggest d_V trait is a good predictor of the variations among growth forms. The lack of difference in d_V functional trait among different zone and existence of significant difference among growth forms imply that the d_V trait reflects a compromise in other functional strategies toward benefiting structural growth. The d_V increases with height to the fourth power (McMahon 1973) therefore any increase in height growth is scaled to an increase in tissue volume of 4th power. It is therefore, plausible that the significant differences in the whole plant functional performance among different growth forms is attributed to the drastic increase in tissue volume associated with heigh growth. Recent studies on the relationship between tree height and hydraulic show that the ratio of thickness of tracheid wall to span of tracheid lumen increased with height and tall trees have large vessels and low vessel density (Preston *et al*. 2006, Woodruff *et al*. 2008). It can be inferred that vessel tissue volume intuitively should increase with tree height. Therefore changes in vessel lumen are more pronounced with increasing tree height, and this may explain why I observed a significant difference in d_V among growth forms (shrub, small-medium trees, large trees).

Relationship between Vessel density and Vessel diameter

Examination of relationship between vessel diameter (d_V, µm) and vessel density (V_d, number vessels mm^{-2}) displayed a significant inverse correlation (Fig. 3.8). Species with highest V_d had corresponding lowest d_V. Vessels with large diameter and pore size in intervessel pit membranes are evolutionarily favoured for efficient water conductance (Tyre *et al*. 1994, Hudson *et al.* 2010). Thus, large vessels allow for low investment in xylem structures while maintaining high conductivity. High salinity environment influences construction of higher abundance and narrower xylem vessels than in nonsaline environment (Kozlowki 1997). My study showed d_V decreased with increasing

V_d and a general trend in which species from the MLT zone (highest salt exposure) had the highest V_d and narrowest d_V and V_d decreased in the landward direction. My observations on the relationships between V_d and d_V are consistent with previous studies (Sobrado 2006, Robert *et al*. 2009, Poorter *et al*. 2010). Changes in the dimensions of vascular elements are considered to be regulated by auxin concentrations (Aloni 1980, Aloni and Zimmermann 1983, Lev-Yadun and Aloni 1995). When production of auxin is high, xylem tissue is composed of many narrower vessels and conversely, plants with low auxin concentration have xylem tissue with fewer and wider vessels (Klee and Estelle 1991). Reduction in the hydraulic dimension through a decrease in d_V and d_h in favor of an increase in number of smaller d_V and d_h is a strategy favoring hydraulic safety, by reducing the risk of xylem embolisms in high saline conditions (Tyre and Sperry 1988, Tyre and Zimmerman 2002).

Relationship between Hydraulic mean diameter, and Vessel density

Relationship between vessel density (V_d, number of vessels mm^{-2}) and hydraulic mean diameter (d_h, µm) displayed a significant inverse correlation (Fig. 3.9). Species with highest V_d had lowest d_h and conversely, species with lowest V_d had the highest d_h (Fig. 3.9). Species with high d_h and low V_d (*Myristica hollrungii, Dolichandrone spathacea, Heritiera littoralis, Cynometra ramiflora*) are UHT and BSM species. These species experience the shortest salt exposure (lowest salt level) and species that experience the longest duration of salt exposure (*Osbornia octodonta, Sonneratia alba,* *Avicennia marina*) exhibited highest vessel density with corresponding low hydraulic mean diameter. My study showed d_h decreased with increasing V_d. There was also a general trend in which species from the MLT zone (highest salt exposure) had the highest V_d and lowest d_h. In addition, V_d decreased in the landward direction. My observations are consistent with previous studies (Sobrado 2006, Robert *et al*. 2009, Poorter *et al*. 2010). Reduction in hydraulic dimension through a decrease in V_d and an increase in d_h is a trade-off between hydraulic safety and efficiency which favors hydraulic efficiency. Fewer vessels with larger d_h is a strategy favoring hydraulic efficiency which subsequently promotes increased growth and productivity. Conversely, construction of many smaller vessels with low d_h is a compromise between hydraulic safety and efficiency. This compromise benefits hydraulic safety by reducing the risk of xylem embolisms in high saline conditions (Tyre and Sperry 1988, Tyre and Zimmerman 2002).

Relationship between Potential hydraulic Conductivity, Zonation, and Growth forms

Potential hydraulic conductance (K_P, kg $m^{-1}s^{-1}MPa^{-1}$) varied among different zones and growth forms (Fig. 3.11, 3.12). However, the mean difference of K_P among zones and growth forms were not significantly different. K_P is positively correlated to growth rate and negatively correlated to P_{wood} (Poorter *et al*. 2010). I observed strong association in the wood hydraulic functional traits (d_V, V_d, d_h, P_{wood}). However, my results showed no difference, and this can be explained by my results in Fig. 3.5, 3.13.

K_P is dependent on d_V and V_d hydraulic trait, and as such the lack of difference in V_d versus growth forms (Fig. 3.12) and d_V vs. zonation (Fig. 3.5) as amounted to no significant difference in K_P among growth forms and zonation.

Relationship between Potential hydraulic Conductivity and Vein density

A linear regression analysis of potential hydraulic conductivity (K_P) against vein density (D_V) showed no significant relationship (Fig. 3.13). The lack of relationship between K_P (kg $m^{-1}s^{-1}MPa^{-1}$) and D_V (mm mm^{-2}) may be a reflection of a trade-off strategy in the whole plant wood and hydraulic functional traits. The coexisting species may have diversified investment strategies involving specialization in other functions, such as mechanical strength, defense, and storage. For example, sapwood is proportioned to serve the function of storage, radial transport, and mechanical functions (Feild and Arens, 2007, Sperry *et al*. 2007, Feild *et al.*, 2009, Hudson *et al*. 2010). These multiple shared functions, therefore, obscure the relationship between vein density (irrigation pipelines) and potential hydraulic conductivity. Additionally, K_P is not correlated to sapwood area (Poorter *et al*. 2010), therefore, K_P cannot translate to a positive relationship with D_V, which is positively correlated to K_L (Fig. 3.14). It is plausible that leaf being a major bottleneck to plant hydraulic conductivity and contributes about 30% of whole plant hydraulic resistance (Sack *et al.* 2003), may also be obscure the link between D_V and K_P. My data indicated that K_P does not correlate to D_V, a trait that is correlate to photosynthetic gas exchange capacity, productivity and growth (Brodribb *et* *al*. 2007, Brodribb and Feild 2010, Feild *et al.* 2011a,b). But suggest that K_L is intimately linked to photosynthesis, productivity, and growth rather than K_P which is consistent with earlier studies (Brodribb *et al*. 2007, Boyce *et al.* 2009, Brodribb and Feild 2010, Feild *et al.* 2011a, b).

Correlation between leaf specific area conductivity and photosynthetic assimilation

Leaf-specific hydraulic conductivity (K_L) of mangroves was positively correlated with maximum rates of net CO_2 assimilation per unit leaf area (A_{max}) indicating a link between A_{max} (µmol CO_2 $m^{-2}s^{-1}$) and K_L (kg $m^{-1}s^{-1}MPa^{-1}$) (Fig. 3.15). My results revealed a mechanistic linkage between leaf area specific conductivity and maximum photosynthesis carbon assimilation. The correlation between K_L and A_{max} suggests that allocation to photosynthetic potential is proportional to maximum water transport capacity. These results of branch water transport capacity (K_L) thus exhibit significant coordination with allocation to potential carbon gain. Additionally, my data indicate that understanding tree hydraulic architecture is critical to insights into comparisons of leaf level measurements among species, and links photosynthetic allocation patterns with branch hydraulic processes. My observations are consistent with previous related studies (Santiago *et al*. 2004, Brodribb *et al*. 2007, Feild and Balun 2008, Zhang *et al*. 2009.)

Relationship between leaf area specific conductivity and vein density

Linear regression analysis of leaf specific area conductivity (K_L) against vein density showed a significant relationship between D_V and K_L (Fig. 3.14). My results are the first to demonstrate this relation for any group of plants. This results supports the hypothesis that the hydraulic capacities at the leaf and stem scales are coordinated. It is interesting this relation occurs in mangrove communities given that mangroves experience drought due to their hypersaline environment. Differences in operating leaf water potential at peak transpiration could have allowed different scalings between leaf and stem hydraulics. Apparently, such differences in leaf turgor relations do not overstand coordination in leaf and stem xylem hydraulic capacities. Thus, an increase in vein density has a positive impact on the leaf-area-specific hydraulic characteristics. This observation indicates a mechanistic linkage between vein density and leaf-area-specific hydraulic conductivity. Increased vein density leads to increased volume of irrigation pipelines reaching the photosynthetic gas exchange site, which in turn increases rate of photosynthesis carbon assimilation. Over 80% of mangrove species studied have D_V greater than 8 mm mm^{-2}. This mangrove average is similar for that for angiosperms as a whole Boyce *et al*. (2009, Fig.3.8). I found that vein density in the hyperdiverse mangrove communities ranges from a low of 4.84 mm mm^{-2} to a high of 15.24 mm mm^{-2} and a mean of 9.01 mm mm^{-2}. Besides the strong positive correlation between K_L and $D_{V,}$ the wide-ranging D_V classes indicate that mangroves have a wide hydraulic performance.

Relationships between potential hydraulic conductivity and wood structure

My results showed potential hydraulic conductivity (K_P) is inversely correlated to vessel density (V_d). Hydraulic conductivity decreased steadily with increasing vessel density (Fig. 3.16). High K_P values were observed to be associated with low vessel density (V_d) species (*Avicennia officinalis, Heritiera littoralis, Dolichandrone spathacea*, *Cynometra ramiflora*, *Myristica hollrungii*), and the low K_P values were associated with high V_d species (*Avicennia alba, Avicennia marina, Luminitzera racemosa*, *Scyphiphora hydrophyllacea*). The negative relationship between K_P and vessel density is surprising, as vessel density should be positively related to K_P. Possible explanation for this counterintuitive result may be attributed to very strong trade-off between vessel density and vessel diameter (Fig. 3.8). Additionally, hydraulic mean vessel diameter (d_h) is a stronger determinant of K_P than vessel density because conductivity scales with the fourth power of vessel radius and only with the first power of vessel density (Equation 1). The negative correlation also suggests that vessel density constrains physiological function to specific operating ranges. A similar relationship has been observed in previous research (Verheyden *et al*. 2005, Poorter *et al*. 2010).

K_P exhibited a strong positive correlation with d_V, (Fig. 3.17). High K_P was observed in species having high vessel diameter (*Sonneratia alba*, *Avicennia officinalis*, *Heritiera littoralis, Myristica hollrungii*, *Dolichandrone spathacea*, *Excoecaria* *agallocha*, *Cynometra ramiflora*), and low K_P values were observed in d_V species (*Aegiceras corniculatum*, *Luminitzera racemosa*, *Avicennia alba*, *Scyphiphora hydrophyllacea*). My observation of a positive correlation in stem hydraulic traits K_P and d_V are consistent with previous research (James *et al*. 2003, Robert *et al*. 2008, Hudson *et al*. 2010, Poorter *et al*. 2010). However, my finding is contrary to that of Zhang and Cao (2009), who claim there is no correlation between wood density and hydraulic traits. Zhang and Cao conducted their experiment in 17 species of Dipterocarps in a plantation establishment. Because these species are plantation species they have been exposed to uniform silvicultural treatment from nursery to plantation, functional traits being plastic may have converged so much under uniform treatment [therefore are functionally similar.

K_P displayed strong positive correlation with weighted hydraulic mean diameter (d_h,) ($R^2 = 0.78$, $P < 0.0001$, Fig. 3.18). Hydraulic conductivity efficiency is linked to d_h (Fig. 3.18). High K_P was observed in species with high d_h (*Sonneratia alba*, *Avicennia officinalis*, *Heritiera littoralis*, *Myristica hollrungii*, *Dolichandrone spathacea*, *Excoecaria agallocha*, *Cynometra ramiflora*) and low K_P values were observed in low d_h species (*Aegiceras corniculatum*, *Luminitzera racemosa*, *Avicennia alba*, *Scyphiphora hydrophyllacea*). My results showed that xylem anatomy is seemingly modulated by underlying biogeochemical characteristics of the intertidal environment, which lead to a coordinated decline in hydraulic properties toward the seaward direction. This deduction is consistent with previous studies (Wakusima *et al*. 1994, Sobrado 2006, and Verheyden *et al*. 2005).

The data from the wood and hydraulic functional traits (P_{wood}, K_P, K_L) from hyperdiverse mangal systems in New Guinea revealed significant differences in functional performance within their relatively narrow habitat range. The data suggest that mangroves have a wide range of wood traits' allocation between their storage, safety, and hydraulic functions. Mangroves exhibited considerable coordination between wood, hydraulic, and photosynthetic carbon assimilation functional traits. The findings from this study are not congruent with my a priori hypothesis. The trend observed in my study denotes a community that has a characteristically wide functional performance. My results do not support the long held paradigm of mangroves being highly conservative (i.e. high water use efficiency hence low assimilation rate) *sensu* Ball and Farquhar (1984) and Ball *et al*. (1988) and therefore have a single optimum ecophysiological strategy.

Implications for Management of Mangrove Ecosystems

My research demonstrates that mangroves varied markedly in their functional performance despite their inhabiting narrow habitat range. My results suggest that the ecological success of mangrove ecosystems as one of the carbon-rich tropical forests is intertwined in the physiological and functional traits of their constituent plant species. Detailed understanding of the full breadth of ecophysiological and functional performance of species is a requisite to sustainability of mangrove ecosystems. I reiterate that the data from this study add further evidence that it is no longer acceptable to view mangroves as conforming to a single functional stereotype. Instead, I have found evidence for both resource profligate as well as resource conservative mangrove species. A focus on the high species' diversity mangrove forests in New Guinea has allowed for the detection of these diverse co-existing functional types in the mangrove biome for the first time.

I will elaborate on the major findings of this study alongside my leaf-level study reported in Chapter Two, with specific focus on important trends in leaf and wood functional traits uncovered and draw from it important management implications for global mangrove ecosystems in Chapter Four.

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CHAPTER IV: SUMMARY AND CONCLUSIONS

RELATIVE CONTRIBUTIONS OF LEAF AND WOOD FUNCTIONAL TRAITS IN THE PERFORMANCE MANGROVES

INTRODUCTION

Mangroves are intertidal plant communities that grow in the land and sea interface where riverine, wave turbulence, hydrological and tidal fluctuation interplay in shaping different growth forms and vegetation zonation bands. The coexisting species exhibit morphological convergence that has long been speculated to reflect species having similar functional performance, but this is only backed by a few studies from low diversity (two to three species) subtropical communities (Ball and Farquhar 1984, Ball 1988, Ball *et al*. 1988, Sobrado 2000). The functional performance of the species influences the spatial distribution (i.e. pattern of distribution; irregular, regular, and random) of mangroves and subsequently, has a great impact on coastal dynamics and mangroves. My study tested the hypothesis that individual species within hyperdiverse New Guinea mangrove communities have uniformly narrow functional performance despite their widely differing phylogenetic affinities (Fig.3.21). An in-depth review of the overall biological, ecological, and physiological data on the global mangrove community with specific focus on hyperdiverse mangrove communities in New Guinea and their significance in the tropical coastal biogeochemical processes is provided in Chapter I. It was revealed in Chapter 1 that mangroves despite thriving in an environment with an abundance of water experience severe water stress, and have adapted by being highly conservative in their water use strategy (Ball and Farquhar 1984, Ball 1988, Ball *et al*. 1988, Sobrado 2000). To test this hypothesis– that mangroves are highly conservative in water use strategy, I focused on measuring the leaf and photosynthetic gas exchange functional traits across a subset of 15 species from the total of 31 coexisting mangrove species that occur in different zonation bands and exhibit varying growth forms from six hyperdiverse communities in New Guinea (Chapter II). I further investigated the wood anatomy and hydraulic functional performance for these 31 species (Chapter III). This concluding chapter summarizes the main findings from Chapters II and III, provides a synthesis of the previous studies on leaf and wood functional traits, and concludes with practical recommendations for mangrove rehabilitation, restoration, and coastal zone management in Papua New Guinea.

Trade-offs in Hydraulic Efficiency versus Safety

To harvest carbon from the atmosphere, mangroves must lose water. Because plants lose about 90% of water in the process of gaining carbon, plants must maintain a continuous supply of water to gain a productive amount of carbon (Kramer and Boyer 1995, Milburn 1996, Tyree 1997, Meinzer *et al*. 2001). To maintain a positive water balance, mangroves utilizing seawater must regulate salt uptake by the roots, either excluding it from entering the hydraulic stream, secreting it, or accumulating it within the cellular structure and excreting it over time (Ball 1996, Sobrado 2000). The efficiency of the water transport in mangroves is regulated by the cellular structure of wood and leaf functional traits. The variability in leaf and wood anatomy and functional traits has significant influence on the water transport and subsequent effect on efficiency of photosynthesis, productivity, growth, and survival (Sperry 2003, Brodribb *et al*. 2007, Boyce *et al.* 2009, Feild *et al*. 2011a, b). Structural and functional traits are therefore, a reliable source of information on mechanisms enabling plants to adjust to changing environmental conditions along environmental gradients.

The variation in functional performance of mangrove species occupying similar ecological niche, i.e. hypersaline environment reflects the ability of species to adapt to different ecological optima. For example; leaf and wood functional traits though are intimately linked, species may differ in their resource use strategy that may results in differences in rates of carbon assimilation, productivity, and growth rate (Brodribb and Hill 1999, Brodribb and Feild 2000, Brodribb *et al*. 2007, Zhang and Cao 2009, Hudson *et al*. 2010). The wide variation in functional traits and trade-offs between hydraulics, biomechanics, safety, and storages enable species to coexist perpetually in forest communities (Williams *et al*. 1989, Reich 1998, Santiago *et al.* 2004, Aiba and Nakashizuka 2009, Robert *et al*. 2009, Zhang and Cao 2009, Poorter *et al*. 2010). The ability of high number of mangrove species to inhabit a narrow ecological niche (e.g. similar zone) is attributed to the subtle differences in between wood and leaf functional traits.

Study of leaf and wood functional traits is emerging as a promising approach in understanding the full spectrum of functional performance of mangrove species, in particular their resource use strategies involving trade-off between growth, storage, and hydraulic function that link to ecosystem productivity. My two studies clearly demonstrated for the first time that photosynthesis and transpiration are intimately linked to leaf and wood functional traits in mangrove species. I will therefore in the following discussion summarize the major findings of my two studies: diversity of leaf productivity function and coordination in wood hydraulic-mechanical functional performance. I will also summarize the main views of previous related studies to crystallize what are my new findings in refute my a priori hypothesis-'mangroves will exhibit a narrow functional performance range despite their wide phylogenetic affinities'. My new findings refute the hypothesis that mangroves have a narrow functional performance range despite their wide phylogenetic affinities (Fig. 3.21), and replace it with a new view in which mangroves have a wide functional performance, and are both conservative and profligate (liberal) in their resources use strategies.

Diversity of Leaf Productivity Function

Leaf and Photosynthetic functional traits data from previous studies

Leaf traits including photosynthetic carbon assimilation (A_{max}, µmol CO_2 $m^{-1}s^{-1}$), stomatal gas exchange (g_{smax}, mmol H_2O $m^{-2}s^{-1}$), vein density (D_V, mm mm^{-2}), and leaf mass per area (LMA, g m^{-2}) are emerging plant functional traits that predict growth, survival, and productivity of plants (Poorter *et al*. 2009). The differences in these functional traits represent the variation in functional performance of coexisting species within a community or biome and are linked to resource trade-offs reflecting adaptations to resource and environmental gradients (Wilson *et al*. 1999, Vendramini *et al*. 2001, Suárez 2003, Boyce *et al*. 2009, Beer *et al*. 2010, Poorter *et al*. 2010).

Numerous studies have investigated variation in leaf traits and photosynthetic functional traits in land plants from plant assemblages from different biomes (Garnier 1992, Lambers and Poorter 1992, Grime *et al*. 1997, Reich 1998, Wilson *et al*. 1999, Vendramini *et al*. 2001, Brodribb *et al*. 2007, Boyce *et al*. 2009, Poorter *et al*. 2010, Beer *et al*. 2010, Feild *et al*. 2011a, b). Although there is a parallel trend in the research on the leaf and wood level functional studies in mangroves (Attiwal and Clough 1980, Clough *et al*. 1982, Ball and Farquhar 1984, Ball *et al*. 1988, Bunt 1996, Matthijs *et al*. 1999, Sobrado and Ball 1999, Sobrado 2001, Suárez 2003, Sobrado 2004, Rivera-Monroy *et al*. 2004), most of the previous research on mangrove functional ecology has been limited to very few taxa (usually one to two species) and are based on subtropical rather than tropical mangrove communities. The maximum photosynthetic carbon assimilation rate (A_{max}) of the subtropical mangrove species ranged from minimum of < 5.0 µmol CO_2 $m^{-2}s^{-1}$ in *Rhizophora mangle* from South Africa, 5.3 µmol CO_2 $m^{-2}s^{-1}$ in *Avicennia marina* in southern Australia to 19 µmol $CO_2m^{-2}s^{-1}$ in *Kandella obovata* in China. The photosynthetic gas exchange rate declined by ~50% with increasing salinity and wood density increased significantly with salinity. Leaf and wood level functional studies on tropical hyperdiverse mangrove ecosystem have been not yet been done. Therefore, my main purpose was to investigate the relationships among leaf functional traits and zonation bands “that have been shown to reflect biogeochemical factors” and growth forms (Chapter II) to understand the functional performance of the hyperdiverse mangrove ecosystem in New Guinea.

Previous investigations on relationship between K_S and A_{max} and between K_L and A_{max} from tropical rain forest showed positive correlations (Brodribb and Feild 2000, Brodribb and Holbrook 2003). K_S is the meausre of the hydraulic efficiency of a specific sapwood area in conducting water; kg $m^{-1}s^{-1}$ MPa^{-1} which is equivalent to variable K_P used in this my study. My data on relationship between potential sapwood specific area hydraulic conductivity (K_P) and A_{max} showed no correlation, but showed positive correlation between K_L and A_{max}. This lack of relationship between K_P and A_{max} is interesting because all previous studies showed K_P is intimately associated with photosynthetic gas exchange capacity of species. My present findings therefore imply that the xylem sapwood area specific hydraulic conductivity in mangroves is not a good correlate of photosynthetic gas exchange capacity but K_L is, and imply that K_L is a better trait to be used for understanding the relationship between hydraulics and photosynthetic gas exchange rate in mangrove environment.

Trends in Leaf Mass Area from Previous Studies and the Present Study

Leaf mass per area (LMA, g m^{-2}) is a trait strongly correlated to a plant's resource-use strategy, growth, and survival rate (Lambers and Poorter 1992, Grime *et al*. 1997, Reich 1998, Cunningham *et al*. 1999, Wilson *et al*. 1999, Vendramini *et al*. 2002, Beer *et al*. 2010). The general consensus on differences in the LMA trait is that it is modulated by variation in biogeochemical and physical environmental variables: nutrient, salinity, and solar radiation (Cornelissen *et al.* 1997, Westoby 1998, Niinemets 1999, Reich *et al*. 1999, Wilson *et al*. 1999, Niinemets 2001, Poorter *et al.* 2010). LMA is positively related to A_{max} (Reich *et al*. 1995, Poorter and Bongers 2006), CO_2 (Ishizaki *et al*. 2003), aging (Suárez 2003), salinity (Suárez 2005), leaf density (Niinemets 2001, Poorter *et al.* 2010), temperature (Niinemets 2001), and solar irradiance (Niinemets 2001) but inversely related to N content. (Castro-Díez *et al*. 2000). LMA is highly plastic and is greatly influenced by the biophysiochemical environment of a species. LMA also differs among growth forms, with trees and subshrubs (treelets) having higher LMA than shrubs as well as climbers and scramblers (Chapin 1980, Liu *et al*. 2010). Most of the previous work on the LMA trait has focused on land plants, and there are very few studies that are mangrove specific (Suárez 2003, Méndez-Alonzo *et al*. 2008). Even then, these few studies measured LMA from no more than three species that were from low diversity mangrove communities found that LMA increased with salinity. There are no previous LMA data from hyperdiversity mangrove communities and my data (Chapter II) is a first documentation of the leaf-resource-use strategy of hyperdiverse mangrove communities.

My LMA results indicated differences among zonation bands, with species in the mean low tide (MLT) zone exhibiting the highest LMA range (161.91 to 289.00 g m^{-2}); the lowest was in the back swamp mangrove (BSM) zone (93.14 to 117.67 g m^{-2}). The LMA in mangrove is ~ two-fold higher than in temperate forest (40 - 120 g m^{-2}; Reich *et al*. 1991). The LMA trait in mangroves appeared to be moderated by tidal duration which would be consistent with previous studies (Ball and Pidsley, 1995; Sobrado and

Ball 1999, Suárez 2003, 2005). These previous studies found that LMA increased with salinity. Species exposed for the longest duration to salt water yielded higher LMA than those exposed for the shortest duration to daily tides. The high LMA in the MLT zone may also be linked to the compounding effect of low N as a result of lack of organic soil layer, high salinity, and solar radiation.

Comparisons of photosynthetic gas exchange studies of the past in contrast to the present study.

Leaf photosynthetic functional traits (A_{max}, g_{smax}) collectively a good predictor of the carbon assimilation rate, productivity, growth, and survival of a species (Brodribb *et. al*. 2007, Feild and Balun 2008, Brodribb and Feild 2010) and diversification of angiosperm flora (Feild *et al.* 2011a, b). Previous studies of photosynthetic gas exchange rate showed that photosynthetic gas exchange capacity differed markedly across salinity gradient and growth forms. A_{max} and g_{smax} were generally highest in the most exposed zone and decreased in the landward directions (Ball 1988, Passioura *et al.* 1992, Suwa 2011). A_{max} and g_{smax} also varied markedly among growth forms, with the highest records from large trees, followed by small-medium trees and large trees respectively (Ball 1988, Passioura *et al.* 1992, Ball and Pidsley 1995, Clough *et al*. 1982, Clough 1998, Suwa 2011).

My results showed that measured parameters of photosynthetic gas exchange capacity in hyperdiverse mangrove communities in New Guinea differed markedly among zones and growth forms. The A_{max} and g_{smax} were highest in the most sun exposed zone, mean low tide zone, and correlated with high LMA (161.91 to 289.00 g m^{-2}), and is two-fold greater that the temperater forest species (40-120 g m^{-2}). There was a strong coordination between zonation and photosynthetic gas exchange traits. Overall, my study showed that A_{max} and g_{smax} are intimately linked to hydraulic functional traits.

Comparisons on leaf vein density studies of the past to the present study.

Vein density (D_V) functional trait is emerging in importance as a key mechanism in the evolution of high photosynthetic gas exchange rates (Brodribb *et al.* 2007, Boyce *et al*. 2009, Brodribb and Feild 2010, Feild *et al*. 2011a). For example single vein gynosperms have mean D_V of > 5 mm mm^{-2} and mean photosynthetic rates (>8 µmol $CO_2m^{-2}s^{-1}$). Evolution of multiple veins in angiosperm increased the irrigation surface area (available vein surface area through which water travels) in the stomata which have led to a sharp increase in productivity in angiosperm diversification (Feild *et al*. 2011a). Previous study showed A_{max} and g_{smax} increase with D_V, therefore the high vein density in mangrove species are indicative of mangroves having relatively high photosynthesis.

Wood and hydraulic functional traits data from previous studies

Mangroves are challenged daily and seasonally with fluctuations in salinity levels, hydrological perturbations, and fluvial changes inherent with tidal regimes (Semeniuk 1981, Cohen and Lara 2003, Lara and Cohen 2006). For example, 42% of 166 km coastline in Amazonia (North Brazil) retreated as a result of landward sand migration, and invaded 38% of the herbaceous mud flats (Cohen and Lara 2003). Additionally, they are subjected at irregular intervals to short-term hydrology perturbations such as extreme floods and El Nino-related climate changes, which affect inundation time and soil water salinity (Lara and Cohen 2006, Sobrado 2007). These few studies observed V_d increased with salinity, while the d_V and d_h declined (Lara and Cohen 2006, Sobrado 2007). However, there are very little data on the relationship between wood anatomy and hydraulic functional traits for mangrove species (Sperry *et al*. 1988, Sobrado 2007). These few studies are confined to low diversity communities and therefore are limited in their use for making inferences regarding hyperdiverse mangrove communities such as those in New Guinea.

Mangrove species in the hyperdiverse mangrove communities in PNG varied markedly in wood functional traits among different zonation bands, growth forms, and root system types. Mangroves exhibited strong coordination between the wood functional traits (P_{wood}, d_V, V_d, d_h) and hydraulic functional traits (K_P and K_L). Hydraulic conductivity in mangroves has been proposed to be regulated partially by shrinking and swelling of native hydrogels (chain of insoluble polymers) in pit membranes of vessels (López-Portillo *et al*. 2005). At the whole plant level, hydraulic and leaf functional traits are well connected, and the variation in functional traits either at the leaf or wood level determines the functional performance of individual species (Fig.3.14, 3.15). In the following discussion, I will point out the main findings of my two projects (project 1-variation in leaf functional performance and project 2-variation in wood functional traits). I will then relate the management implications of my results for the current mangrove ecosystem restoration programs in Papua New Guinea.

My studies (project 1 and 2) revealed that mangrove species have a much wider functional performance than the current view, i.e., mangroves have narrow functional performance. For example, species with high photosynthetic assimilation rates; *Avicennia marina* (19 µmol $CO_2m^{-2}\,s^{-1}$), *Aegialitis annulata* (17 µmol $CO_2m^{-2}s^{-1}$), and *Sonneratia alba* (17 µmol $CO_2m^{-2}\,s^{-1}$), seemed to have different trade-off strategies to achieving the common goals of increased photosynthesis (A_{max}), productivity, growth, and survival. The *Sonneratia alba* invested more highly on hydraulic efficiency (three-fold K_P, 113 kg $m^{-1}s^{-1}MPa^{-1}$) than the former two species; 48 kg $m^{-1}s^{-1}MPa^{-1}$ and 45 kg $m^{-1}s^{-1}$ MPa^{-1} respectively. K_P has been shown in previous studies to correlate positively with growth (Poorter *et al. 2010*), however, my study did not show any correlation between A_{max} and K_P. K_P is the measure of potential sapwood area specific hydraulic conductivity (kg $m^{-2}s^{-1}MPa^{-1}$):-theoritical measure of hydraulic efficiency of specific xylem area in conducting water. K_L, measures the capacity of a xylem area to support the hydraulic demand of a given leaf area (kg $m^{-2}s^{-1}MPa^{-1}$). K_L (not K_P) is correlated to photosynthetic gas exchange capacity of species. The former two species attained high assimilation rates by investing in increasing irrigation network (vein density) in the photosynthetic gas exchange site, which subsequently lead to high productivity and growth. The two former species had a D_V of 15.2 and 14.0 mm mm^{-2} respectively, which is 27% above *Sonneratia alba*. The maximum D_V values in mangrove species are lower than, but overlap with that of tropical rain forest species (13 to 23 mm mm^{-2}; Feild *et al.* 2011). The D_V (Table 2.4) for the 31 mangrove species are about three-fold higher than that of gymnosperms (mean ~ < 5 mm mm^{-2}) (Brodribb *et al*. 2007, Feild *et al*. 2011).

Leaf photosynthetic gas exchange capacity is modulated by wood hydraulic functional traits

Leaves lose large amounts of water to gain very little carbon, a trade-off that makes rapid transpiration a prerequisite for high productivity (Cowan and Farquhar 1977, Kramer and Boyer 1995, Meinzer *et al.* 2001). However, this requisite for high productivity is counterintuitive in mangrove systems, because being in a hypersaline environment, salt free water is limited. Therefore, mangroves are generally adapted to being more conservative in their water use, i.e. they have high water use efficiency. Intuitively, a decrease in water intake leads to a decline in transpiration, which consequently leads to low carbon gain. This logic has shaped the present paradigm in which mangroves have high water use efficiency and consequently, narrow functional performance (Ball 1988, Ball *et al*. 1988, Ball and Farquhar 1984, Ball 1996, Sobrado 2000).

My studies on leaf and photosynthetic functional traits, and wood and stem hydraulic functional traits relations among zonation bands, growth forms and root system types of 31 mangrove species showed significant differences (Table 2.3, 3.0). The results provided strong evidence that mangrove species possess a wide range of functional performance. The results showed leaf photosynthesis, productivity, and growth are correlated to wood and stem hydraulic functional traits, and the differences in assimilation rates represent the variation in wood anatomy and hydraulic functional traits. Leaf and wood functional traits affect the way plants tolerate environmental stresses and therefore contribute to shaping of the distribution patterns of mangrove species across the biogeochemical environmental gradient.

It is well established that there is a strong correlation between plant hydraulic functional traits (K_L,V_d, d_h, d_V) and photosynthetic gas exchange capacity (A_{max}, g_{smax}) (Meinzer and Grantz 1990, Meinzer *et al*. 1995, Sperry 2000, Brodribb and Feild 2000, Brodribb *et al*. 2007). Recent studies showed a strong positive correlation between D_V and A_{max}, g_{smax} (Brodribb *et al*. 2007, Boyce *et al.* 2009, Brodribb and Feild 2010, Feild *et al*. 2011a, b). These studies showed that an increase in D_V results in drawing higher xylem base hydraulic irrigation closer to the photosynthetic gas exchange site in the leaf, which subsequently increases the rate of photosynthesis, productivity, growth, and survival rates. My results on D_V and the relation between photosynthetic traits (A_{max}, g_{smax}) conforms to these earlier studies, but also shows strong evidence that the hydraulic functional traits in mangroves differ significantly along biogeochemical gradients, root system types, and growth forms. My results overall failed to support the hypothesis that hyperdiverse mangrove communities in New Guinea exhibit a narrow leaf photosynthetic and stem hydraulic functional performance. Instead, they present strong evidence that mangrove species exhibit characteristics of profligate resource use strategies as well as resource conservation strategies. My study showed profligate and conservative mangrove species coexist.

Present paradigm on functional performance of mangrove ecosystem and my hypothesis

The notion that mangroves have narrow functional performance implicates species having similar leaf photosynthetic and wood hydraulic functional traits. Any differences in functional performance represent variation in physiological and functional traits. For example, tropical rain forest species exhibit Amax of ~ 5 to 23 $\mu molCO_2m^{-2}s^{-1}$ (Brodribb *et al*. 2007, Feild *et al*. 2011).

Recapitulating on the current widely held paradigm, I hypothesized that the hyperdiverse mangrove communities in New Guinea despite having diverse phylogenetic affinities exhibit a narrow functional performance. I hypothesized specifically that: 1) the 31 mangroves species from New Guinea should have similar leaf (D_V, LMA) and leaf photosynthetic functional (A_{max}, g_{smax}) traits and subsequently have a low photosynthetic gas exchange rate, and 2) the 31 mangrove species should have a similar wood anatomy (P_{wood}, d_V, V_d, d_h) and wood functional (K_P, K_L) traits and therefore have narrow functional performance.

The specific objectives of my two studies were as follows: 1) investigate the relationship in leaf and photosynthetic functional traits among different zonation bands and growth forms in six hyperdiverse mangrove communities in New Guinea; 2) investigate the relationship in wood and xylem hydraulic functional traits among different zonation bands, growth forms, and root system types in six hyperdiverse mangroves communities in New Guinea; and 3) investigate the relation of hydraulic functional traits to leaf photosynthetic gas exchange properties in six hyperdiverse mangrove communities in New Guinea.

Major trends unravelled from my studies

The big picture of the leaf and photosynthetic functional performance from my study is that mangroves have wide functional performance, for example; I measured photosynthetic gas exchange capacity ranging from 4.84 to 19.2 $\mu molCO_2m^{-2}s^{-1}$ which is relatively wide in contrast to an A_{max} measurement range of 5 to >8 $\mu molCO_2m^{-2}s^{-1}$ from the subtropical mangrove communities (Ball and Farquhar 1984). Mangroves differed in their functional performance among different zonation bands. Species in the mean low tide (MLT) zone featured the highest net maximum photosynthetic carbon assimilation and stomatal conductance rate and leaf mass per area (LMA). These photosynthetic and leaf resources that use strategy traits showed a declining trend in the landward direction. These same leaf photosynthetic traits varied significantly among different growth forms. Mangroves therefore generally have a wide functional performance despite growing in a narrow ecological range.

My leaf level study on the photosynthetic functional performance uncovered for the first time, strong evidence of mangrove species exhibiting marked differences in functional performance along zonation bands and among different growth forms. Some species exhibited a profligate and some conservative resource use behaviour. Species with low photosynthetic gas exchange capacity and high water use efficiency are considered conservative in their resource use strategies and those that have high photosynthetic gas exchange capacity and low water use efficiency are considered as profligate (liberal in their resource use strategies) (Ball and Farquhar 1984, Sobrado 2001).

Leaf mass per area (LMA), an important trait in plant growth and an important indicator of plant resource use strategy has mostly been involved with mesophytes, and very few investigated halophytes including mangroves (Suárez 2003, Méndez-Alonzo and López-Portillo 2008). Previous LMA data on mangroves are based on less than three species and apparently no one has looked at LMA differences among different zonation bands and growth forms. My data represent the first comprehensive measurement of patterns in LMA across hyperdiverse mangrove communities. My study revealed that LMA was highest in the MLT zone and declined in the landward direction, indicating a strong correlation between the LMA trait and biogeochemical factors represented by different zones. My results indicated that mangroves in MLT zone (high salinity site) have high carbon investment leaf construction than those in low salinity zone. Because the MLT zone has the least organic soil layer and nutrient, mangroves in MLT zone invest high in the leaf construction cost which lead to longer leaf life span (i.e. reduced leaf turn over rate), and the opposite strategy may be observed by species in low salinity zones.

My results indicated that the distribution of mangrove species is correlated to the biogeochemical environmental gradient and the species distribution pattern represents the variation in functional traits. The whole plant photosynthetic gas exchange capacity, productivity, growth, and survival are modulated by leaf photosynthetic and hydraulic functional traits.

Wood density (P_{wood}) differed significantly across biogeochemical environmental gradient and RSTs. P_{wood} was highest in the MLT zone and decreased in the landward direction (Table 3.0). Across species, photosynthesis, productivity, and growth rate correlated positively with calculated specific leaf area conductivity (K_L, kg $m^{-1}s^{-1}MPa^{-1}$), but showed no relationship between potential specific hydraulic conductance (K_P) (Table 3.0). High P_{wood} favors hydraulic safety and low P_{wood} favors hydraulic efficiency, therefore investment in constructing high density wood is a strategy favoring mechanical allow safety and hydraulic safety, in the high density wood reduces likelihood of cavitation. Low density wood frees up relative xylem packing area and allows fewer vessel elements to increase dimensions (vessel diameter, mean hydraulic vessel diameter) that lead may lead to drastic increase in hydraulic efficiency.

My studies revealed that mangrove species are able to coexist successfully within a narrow ecological range because each species has distinct ecological, physiological, and functional performance ranges across the biogeochemical environmental gradient. My results indicate vigorous restoration of degraded forest areas will require sound data on the ecophysiological and functional traits of species (autecology).

My studies showed that different growth forms differ significantly in their functional performance. Different growth forms differed in leaf photosynthetic gas exchange and wood hydraulic traits, and these differences are linked to the biogeochemical gradient (Fig.2.7, 2.9, 3.7, Table 2.3, 3.2, 3.3). It is recommended that rehabilitation and restoration programs of degraded mangrove areas consider the growth habit data of species in line with other ecophysiological and functional characteristics.

My studies revealed that aerial root system types (RSTs) differed in their dominance across the biogeochemical environmental gradient. For example, species with stilt/prop root RST are predominant in the mean low tide (MLT) zone and unbuttressed species are confined to upper high tide (UHT) and back swamp mangrove (BSM) zones. Species with stilt root RST had lower P_{wood} and V_d than pneumatophore RST.

Strengths and limitations of research

Most of the data on ecological, physiological, and functional performance of mangrove ecosystems are from glass house experiments and subtropical low diversity communities. Therefore, these studies are limited in their application for drawing inferences for the vast areas of high diversity tropical mangrove communities. My studies differ from most of the previous research in that they are field-based and cover ~ 66% (31 species) of global mangrove species, therefore, supplement previous studies on both high diversity and low diversity mangal communities.

There are no previous studies on the relationship between rooting architecture and functional performance in mangroves. My study is the first to demonstrate that leaf level hydraulic photosynthetic gas exchange capacity of mangroves is partly influenced by the rooting architecture in mangroves. P_{wood} trait which had an inverse relationship with hydraulic conductivity was consistently different for the five root system types (RSTs)

(Fig. 3.3, table 3.1). For example, pneumatophore RST has the highest P_{wood} (0.76 g m^{-3}) and therefore should have the highest vessel density (V_d) yet a low density (0.70 g cm^{-3}) unbuttressed RST has the highest V_d (95.5 vessels mm^2) compared to 67.64 vessels mm^{-2} (Fig.3.19) in a pneumatophore. The stilt root/prop RST is predominantly found in the most unstable zone (MLT) and therefore intuitively should have higher investment on P_{wood} for mechanical safety, but instead has the lowest P_{wood} of the RSTs and highest d_V. This low resource investment in P_{wood} in favor of high d_V by the stilt/prop RST indicate a trade-off between mechanical support and hydraulic efficiency, that is achieved by stilt/prop RST providing mechanical support to the main stem, which then freed the wood to invest higher on hydraulic functions.

Future research on the functional performance of mangal systems should investigate the trade-offs at the tissue level between mechanical and hydraulic functional traits among different root system types (RSTs). This research would provide necessary data for selection of appropriate species to combat storm surges, tsunamis, and tidal waves. Future research should also include chemical analysis of the substrates at different zones to understand the potential effects that nutrients, pH, and salinity may have on mangrove productivity. Spatial distribution patterns of mangroves are linked to the underlying geochemical factors, including pH, nutrient, and salinity (Wakushima *et al*. 1994). Therefore, it would be critical to understanding these factors in relation to species distribution to make appropriate choices in selection of species to introduce in rehabilitation programs. Future research should also investigate question on the extent to which the species modify their own environment, rather than passively inhabit an environment which is already there. As you point out, this is a dynamic environment, so it might be expected that mangroves themselves would have some input.

ECOLOGICAL AND MANAGEMENT IMPLICATIONS

Papua New Guinea (PNG) is in the geo-climatic region that is prone to natural hazards such as volcanic eruptions, tsunamis, river and coastal flooding, landslides, tropical cyclones, climate change, sea level rise or sea swells and droughts. The coastal areas of PNG are the most vulnerable to these weather extremes and inundation, yet a lot of local human communities are located along this area (Pernetta and Osborne 1988). Mangrove ecosystems are widely reported to protect coastlines from these natural hazards, notably; tsunamis, river and coastal flooding, tropical cyclones, and sea-level rise; subsequently protecting many human lives (Giensen *et al*. 2007). Rehabilitation of degraded mangrove coastlines is therefore critical to building safe and sustainable coastal communities in view of the global change (Giesen *et al*. 2007). Mangroves occupy a physiologically unique environment, and therefore a detail understanding of their biophysiochemical environment would be important for successful rehabilitation. Mangrove restoration is embraced in the Papua New Guineas' natural disaster contingency planning program under the United Nations' charter (Gilman *et al*. 2006). Mangroves as revealed in my studies are all 'doing things differently', and physiologically appear to be well differentiated along the biogeochemical environmental gradient. Therefore they are not just 'plug and play' plant assemblages that can be plugged out randomly for restoration of coastlines. The success of the United Nations' chartered mangrove restoration program for Papua New Guinea will require a scientifically based rehabilitation prescription. Notably, incorporation of my present data on the ecophysiological functional performance of mangrove species from the hyperdiverse New Guinea mangrove communities will be critical for establishment of sustainable mangrove restoration programs.

Mangroves have a relatively high seedling mortality rate that varies among species; for example, *Avicennia marina, Ceriops tagal,* and *Rhizopohora stylosa* have 22%, 36%, and 72% seedling mortality respectively (Hutchings and Saenger 1987). Generally mangroves have high mortality rate (Delgado *et al.* 1999) and this has been a major cause of failures in mangrove afforestation and rehabilitation programs. My study did not focus on the functional performance of seedlings. Nevertheless, it would be important from the onset of any habitat restoration and afforestation program to have a good understanding of the seedling autecology of species, especially the physiological and functional traits' relations.

Tide and wave action along with substrate instability all have a major influence on successful mangrove regeneration. Different species have adopted strategies to enhance successful recruitment that vary in terms of seed development, size, and number. Therefore, selected species should be raised in seedling nurseries to desirable size prior to transplanting to increase survival rate. Afforestation in the uninhabited coastlines can have successful establishments if species are planted based on their site-specific prescriptions (Table 4.0). In highly exposed sites, root systems of some species have better anchorage than others, while others may be better at acquiring nutrients from the sediment, or oxygen from the air. For example, stilt or prop roots of *Rhizophora* spp offer mechanical support to tall trees to withstand the storm surges, tidal waves, strong winds (Field 1995). For *Avicennia* and *Sonneratia* which grow at mean lower tide zones, pneumatophores aim to acquire atmospheric oxygen (Field 1995). The periderms and cortex of stilt root of *Rhizophora* spp contain a lot of tannin that contribute to the solidity of roots while pneumatophores of *Avicennia* consist of aerenchymatous tissue containing many air spaces for oxygen reserve (Komkris 1993).

Functional traits hold the key to sustainable restoration of degraded mangal systems

Mangrove restoration and rehabilitation is a new concept in Papua New Guinea and was adopted when the loss in mangrove forests became apparent as a result of unsustainable exploitation. This has resulted in decline in the coastal fisheries productivity, loss of livelihood of coastal communities, and loss of homes in traditional communities due to rise in sea-level (Banka *pers.comm*). Rehabilitation of mangrove ecosystems is often recommended when the ecosystem has been altered to such an extent that it cannot regenerate naturally. The success of rehabilitation and restoration of mangroves is possible when the original ecophysiological and functional characteristics of species are known and adopted in a replanting program. Presently, there are no such data for the hyperdiverse mangrove communities in New Guinea, and the present rehabilitation and restoration initiatives are carried out on an ad hoc basis. Results from my studies on leaf and wood level functional traits' relations will play a key role in sustainable rehabilitation initiatives. The present rehabilitation and restoration initiatives by World Wildlife Fund for Nature (WWF), University of Papua New Guinea, and the National Department of Environment and Conservation carried out under United Nation charter lack a scientific framework. My data are able to recognize species into their potential site-specific requirements. For example, the 31 species in my studies are listed into different growth categories (Table 4.0). Species are listed as 1st and 2nd choices for rehabilitation (replanting degraded mangrove areas), afforestation (introduction of mangrove to uninhabited coastal areas) programs based on their functional performance. I envisioned that my data will increase the likelihood that a successful strategy is adopted, and sooner rather than later.

Table 4.0: Recommended site-specific species listing for rehabilitation and afforestation of degraded mangrove forest and uninhabited coastlines in Papua New Guinea. Species labelled with superscript 1 and 2 refers to 1st and 2nd choice for the given site. Species with superscript 1R indicates, particular species should be planted along the river banks.

Mudflats in MLT Zone	**Sand dunes in MLT Zone**	**UHT/BSM Zone**
Rhizophora stylosa^{1} Griff.	*Avicennia marina*^{1} (Forssk.) Vierh.	*Xylocarpus* spp^{1}
Sonneratia alba^{1} Sm.	*Sonneratia alba*^{1} Sm.	*Heritiera littoralis*^{1} Ait
Avicennia marina^{2} (Forssk.) Vierh.	*Osbornia octodonta*^{1} F. Muell.	*Bruguiera gymnorrhiza*^{1} (L.) Lam
Avicennia alba^{2} Blume	*Aegialitis annulata*^{1} R. Br.	*Ceriops tagal*^{1} (Perr.) C.B.Rob.
Avicennia officinalis^{2}	*Pemphis acidula*^{1} J.R. Forst & G. Forst	*Myristica hollrungii*^{1} Warb.
Rhizophora apiculata^{2} Blume	*Rhizophora stylosa*^{1}	*Nypa fruticans*^{1R}Wurmb
	Ceriops tagal^{2} (Perr.) C.B.Rob.	*Bruguiera parviflora* (Roxb.)Wight & Arn. Ex Griff.

Publication of my data and awareness to local communities

I envisage publishing the results of my two projects in three separate papers. In paper one; I intend to title it ‘variation in leaf traits and photosynthetic functional traits among different zones and growth forms in six hyperdiverse mangrove communities in New Guinea’. In paper two, I intend to title it ‘variation in wood anatomy and wood hydraulic functional traits among different zones and growth forms in six hyperdiverse mangrove communities in New Guinea’. In paper three I proposed to title it ‘leaf photosynthetic gas exchange and wood hydraulic functional traits in the hyperdiverse mangrove communities are well coordinated’.

Local communities will be made aware of the significance of mangrove in sustaining the fresh and marine water biodiversity which has long sustained traditional societies globally and the potential consequence of degradation of the mangrove communities. Including increase threat to safety to coastal communities against natural hazards such as tsunami, storm surges, tidal waves and shoreline erosion. Communities will be made aware of how mangrove losses will lead to reduction in coastal water quality, biodiversity, fish nursery habitat and fish catches.

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Vita

Lawong Balun was born June 29, 1962 to Balun and Marawe Garap of Sangana village, Karkar Island, Madang Province, Papua New Guinea (PNG). He attended Taleng Primary School and graduated in 1974 and did his High School in Karkar High School and graduated in 1978. He then attended Senior High School in Passam National High and graduated in 1980. Lawong attended University of Papua New Guinea (UPNG) in Port Moresby, PNG, and graduated 1989 with a Bachelor of Science degree. He then took up Post Graduate Diploma in Science (PGDSc) in UPNG and graduated in 1991. Upon graduating with PGDSc in UPNG Lawong taught as a lecturer in Papua New Guinea University of Technology (PNGUOT), in Lae, Papua New Guinea. Lawong won a scholarship to do Masters in the University of Edinburgh, Scotland, in 1995 and graduated in 1996. Upon graduation from University of Edinburgh, Lawong returned to lecturing duties at PNGUOT, Lae, Morobe Province, PNG. Balun accepted a teaching assistantship in the Department of Ecology and Evolutionary Biology in 2008. He earned his Doctor of Philosophy degree in Ecology and Evolutionary Biology in July 2011. In Fall 2011, Lawong will return to take up his lecturing job with the Forestry Department at PNGUOT, Lae, Morobe Province, PNG.