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How are anatomical and hydraulic features of *Avicennia marina* and *Rhizophora mucronata* trees influenced by siltation?

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‘IF I have seen further it is by standing on ye sholders of Giants’

(Isaac Newton,15 February 1676)

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Abstract

Mangrove ecosystems are known as very unique ecosystems with a large biodiversity, dominating the coastal zones in tropical and subtropical regions. The mangrove trees have typical characteristics to survive in a salty environment which is subjected to tides of the oceans, seas or rivers. Pneumatophores, salt glands, salt exclusion and vivipary are some adaptations that can be found among the mangrove species. Mangroves are important and essential ecosystems. For example, they function as a sediment trap preventing the destruction of coral reefs and sea grass beds, they house many different and endangered species and they are excellent fish nurseries. The local people depend on the mangrove forests for timber, charcoal and food. Despite, large scale destruction and fragmentation among mangrove forests are observed. Mangroves are even destroyed at a higher rate compared to tropical rainforests and coral reefs. This destruction is caused by intensive cutting, land use changes by humans, pollution, shrimp ponds and oil spills. Accumulating evidence points out that the siltation process particularly causing high tree mortality mangroves. Due to siltation, high amounts of suspended particles cover and thus smother the roots causing oxygen deficiency and possible death of the trees.

The aim of this study was to investigate whether siltation causes stress in mangrove trees and in the worst tree mortality. It was investigated how siltation influenced the physiological and anatomical properties of the trees. Therefore, a measuring campaign was performed in the mangrove forest of Mikindani, near Mombasa (Kenya) from 10 of July till 15 August 2011. This region is known to be silted due to a flush flood in 1997 and the recent land use changes which induce anthropogenic land erosion and run off. A difference in siltation degree was observed in the region and correspondingly the region was divided in high siltation sites and low siltation sites. Measurements were performed on two local and abundant species, *Avicennia marina* and *Rhizophora mucronata*.

The measurements can roughly been subdivided in two parts. First, the diurnal patterns of stomatal conductance and o hydraulic branch conductance were measured using a porometer (AP4) and by applying the field method, respectively. A decline of one or both of these physiological variables indicates more stressful conditions for the tree due to siltation. Secondly, it was studied how trees adapt their anatomical and morphological characteristics in an attempt to prevent fluctuations in their metabolic and ecophysiological pathways due to siltation. Area and density of both vessels and stomata were measured together with other characteristics such as leaf number and sizes. The amount of available oxygen for the roots was estimated by the amount of crab burrows and pneumatophores.

Lower values of stomatal conductance were found in the high siltation sites indicating that siltation causes higher stress levels in trees. The stomatal conductance of *Avicennia marina* was abnormally high in the morning. No significant differences in hydraulic branch conductance were found between sites and species during this study. However, during the measurements of hydraulic conductance water flowing in the opposite direction was more observed in branches collected in the highly silted sites, indicating also more stressed levels. Consistent or significant differences of anatomical features were observed between high and low siltation sites. Some adaptations to siltation were found for both species, whereas others were species-specific. Both the number of crab burrows and the number of pneumatophores were lower in the high siltation sites.

It is hypothesized that the high morning values of stomatal conductance for *Avicennia* result from fresh water uptake by the leaves from dew which probably condensed on the leaves in the early morning. Due to the high salinity in the xylem sap, an osmotic gradient probably pulls the external fresh water through the stomata into the internal tissues. In addition, the water flows observed in the opposite direction during the hydraulic conductance measurements are presumably caused by the high amount of dehydrated cells in the branches. Dehydration of cells is higher in silted trees, since water supply is lower or even absent. The dehydrated cell attract water by creating an osmotic gradient. When the xylem sap flow is not sufficient and fast enough to neutralise this osmotic gradient, other water sources, such as water from the leaves or in the case of the experiment, water from the loading dye are drawn towards the dehydrated cells. Moreover, trees subjected to siltation have higher water us efficiencies. This is concluded from the combined changes in anatomical and morphological characteristics such as smaller and more leaves, smaller stomatal area, lower leaf water content and a better vessel-leaf correlation. To cope with siltation stress, *Avicennia marina* trees adapt their stomatal anatomy by increasing the stomatal density and pore area index. In addition, they protect themself against cavitation by producing smaller vessels and a higher phloem ratio. In response to siltation, *Rhizophora mucronata* trees adapted their vessel anatomy: an increase in vessel density and total lumen area were found in the high siltation sites. Furthermore, the decrease of crab burrows in the silted sites is probably due to the changed soil texture, hindering crabs for digging holes. Pneumatophores are most likely covered by siltation, decreasing the number of pen roots counted in the high siltation site.

In conclusion, siltation imposed water and oxygen stress in both studied mangrove species. Both species responded in a similar way to siltation such as smaller stomata and more and smaller leaves for trees in high siltation sites. Although, some adaptations are species-specific, including the increased vessel density for *Rhizophora* and the higher stomatal density for *Avicennia* found in the high siltation sites. Mangroves are thus negatively influenced by siltation and the trees will adapt their anatomical and physiological characteristics. The interesting hypothesis of water uptake by the leaves within *Avicennia marina* trees needs further research.

Samenvatting

Mangrove ecosystemen staan gekend als zeer unieke ecosystemen met een hoge biodiversiteit. Ze domineren in de kustzones van tropische en subtropische gebieden. De mangrove bomen hebben typische karakteristieken om te overleven in een zout milieu dat onderhevig is aan de getijdewerking van oceanen, zeeën en rivieren. Pneumatoforen, zoutklieren, zout exclusie en viviparie zijn enkele adaptaties die worden aangetroffen onder de mangrove soorten. Mangroves zijn belangrijke en essentiële ecosystemen. ze functioneren bijvoorbeeld als een val voor sediment en beschermen zo de koraalriffen en zeegrasbedden van vernieling, ze zijn een huisvesting voor vele verschillende en bedreigde soorten en ze zijn ideaal als paaiplaats voor vissen. De lokale bevolking is afhankelijk van de mangrove wouden voor hun hout, houtskool en voedsel. Desondanks wordt grootschalige verwoesting en fragmentatie van de mangrove wouden waargenomen. Bovendien worden mangroves vernietigd tegen een hogere snelheid in vergelijking met tropische regenwouden en koraalriffen. Deze vernieling wordt veroorzaakt door intensieve houtkap, veranderingen in landgebruik door mensen, vervuiling, garnaal/scampi-kwekerijen en olielozingen. Accumulerende bewijzen wijzen erop dat het proces van aanslibbing hoge mortaliteit onder de mangrove bomen zou veroorzaken. Door aanslibbing bedekken grote hoeveelheden opgeloste partikels de wortels en verstikken deze door zuurstofgebrek, wat uiteindelijk kan leiden tot sterfte van de boom.

Het doel van deze studie was het onderzoeken of aanslibbing stress en in het ergste geval de dood van mangrove bomen, veroorzaakt. Er werd bestudeerd hoe aanslibbing de fysiologische en anatomische eigenschappen van de bomen beïnvloedt. Hiervoor werd een meetcampagne uitgevoerd in het mangrove woud van Mikindani, dichtbij Mombasa (Kenia) van 10 juli tot 15 augustus 2012. Deze regio staat gekend als zijnde aangeslibd door de vloedgolf in 1997 en door de recente veranderingen in landgebruik die aanleiding geven tot antropogene erosie en run-off. Er werd een verschil in aanslibbing graad binnen het gebied geobserveerd waardoor het gebied werd opgedeeld in een hoge aanslibbing en een lage aanslibbing site. Metingen werden uitgevoerd op twee lokale en abundante soorten, *Avicennia marina* en *Rhizophora mucronata.*

De metingen kunnen ruwweg worden opgedeeld in twee delen. Vooreerst werd de dagelijkse patronen van stomatale conductiviteit en hydraulische tak conductiviteit gemeten door respectievelijk gebruik te maken van een porometer (AP4) en de veldmethode. Een daling in beide fysiologische variabelen wijst op de meer stressvolle condities voor een boom door het proces van aanslibbing. Ten tweede werd er bestudeerd hoe bomen hun anatomische en morfologische karakteristieken aanpassen in een poging om fluctuaties in metabolische en ecofysiologische pathways, veroorzaakt door aanslibbing, te verhinderen. Oppervlakte en densiteit van zowel vaten als van stomata werden opgemeten evenals andere karakteristieken, zoals het aantal en de grootte van de bladeren. De hoeveelheid aan beschikbare zuurstof voor de wortels werd geschat aan de hand van het aantal pneumatoforen en het aantal holen van krabben.

Lagere waarden voor stomatale conductiviteit werden aangetroffen in de hoge aanslibbing sites, wat erop wijst dat aanslibbing hogere stress niveaus creëert in bomen. ’s Ochtends werd een abnormaal hoge stomatale conductiviteit van *Avidennia marina* gevonden.. Gedurende de studie werden geen significante verschillen gevonden in hydraulische conductiviteit tussen de sites en de soorten. Echter gedurende de metingen van hydraulische conductiviteit werden meer waterstromingen in

tegengestelde richting geobserveerd in takken verzameld uit de hoge aanslibbing sites, wat ook wijst op hogere stressniveaus. Consistente of significante verschillen in anatomische karakteristieken werden waargenomen tussen hoge en lage aanslibbing sites. Sommige aanpassingen voor aanslibbing werden gevonden voor beide soorten, terwijl andere soort-specifiek waren. Zowel het aantal holen van krabben als het aantal pneumatoforen was lager in de hoge aanslibbing sites.

De voorgestelde hypothese stelt dat de hoge ochtend waarden van stomatale conductiviteit bij *Avicennia* resulteren uit de opname van zoet water via de bladeren, wat afkomstig zou zijn van dauw dat waarschijnlijk in de vroege ochtend condenseert op de bladeren. Door de hoge saliniteit in het xyleem sap zal een osmotische gradiënt het externe zoet water doorheen de stomata trekken tot in de interne weefsels. Daarnaast werden de tegengestelde waterstromingen, geobserveerd tijdens de hydraulische tak conductiviteit, wellicht veroorzaakt door de hoge hoeveelheid aan gedehydrateerde cellen in de takken. Dehydratatie van cellen is hoger voor aangeslibde bomen aangezien de water aanvoer lager, tot zelf afwezig, is. De gedehydrateerde cellen trekken water aan door het creëren van een osmotische gradiënt. Wanneer de xyleem sapstroom niet bevredigend en snel genoeg is voor de neutralisatie van deze osmotische gradiënt, dan zullen andere bronnen van water, zoals het water in de bladeren of zoals in het geval bij dit experiment, water van de kleurvloeistof, worden aangetrokken naar de gedehydrateerde cellen. Bovendien hebben bomen, die onderhevig zijn aan aanslibbing, een hogere efficiëntie van watergebruik. Dit wordt geconcludeerd uit de gecombineerde veranderingen in anatomische en morfologische karakteristieken, zoals kleinere en meer bladeren, kleinere stomatale oppervlakte, lagere bladwaterinhoud en een betere vat-blad correlatie. Om het hoofd te bieden aan aanslibbing stress, passen *Avicennia marina* bomen hun stomatale anatomie aan door het verhogen van de stomatale densiteit en pore-area index. Daarnaast beschermen zij zichzelf tegen cavitatie door de productie van kleinere vaten en een hogere floëem ratio. Als antwoord op aanslibbing zullen *Rhizophora mucronata* bomen daarentegen hun vat anatomie aanpassen: een toename in vat densiteit en totale lumen-area werd aangetroffen in hoge aanslibbing sites. Bovendien is de afname in krab holen in de aangeslibde sites waarschijnlijk te wijten aan de veranderde bodem textuur die de krabben hinderen bij het graven van holen. De pneumatoforen zijn hoogst waarschijnlijk bedekt door sediment, wat het aantal luchtwortels in de hoge aanslibbing site doet dalen.

Concluderend dat aanslibbing water en zuurstof stress oplegt voor beide bestudeerde mangrove soorten. Beide soorten reageerden op gelijke manier op aanslibbing door bijvoorbeeld kleinere stomata en kleinere maar meerdere bladeren te vormen. Echter waren sommige adaptaties soort-specifiek zijn, zo werden hogere vatendensiteit bij *Rhizophora* en hogere stomatale densiteiten bij *Avicennia* aangetroffen in de hoog aangeslibde sites. De mangrovebomen worden dus negatief beïnvloed door aanslibbing waarop de bomen hun anatomie en fysiologie zullen op aanpassen. Meer onderzoek naar de interessante hypothese van wateropname via de bladeren bij *Avicennia marina* bomen is nodig.

Contents

Introduction

Only when the last tree has died and the last river been poisoned and the last fish been caught will we realise we cannot eat money

(Cree Indian Proverb)

We can no longer ignore the fact that since mankind walks the earth, we want to control nature and mould it to our wishes. Economical and short term profits are mostly preferred over more sustainable and ecological alternatives. All over the world, nature draws the shortest straw and a fast decline of most ecosystems is observed, many species are threatened or already extinct, leaving nothing but the shameful truth as a legacy for future generations. When we forget to think of our future generations, makes it only more certain that they will remember our actions. But the tides can still be turned to the better. Mankind has proven his intelligence and creativity many times in history. Step by step we can restore the natural order in this world so future generations will not have to carry the burden of our selfishness.

One of world most threatened ecosystems by mankind are the mangroves, found at the costal zones in the tropical and subtropical regions. Their economic and ecological use is highly valuable making many animals and local communities dependable on these forests. Despite it all, a fast decline and fragmentation are a matter of concern for this unique and biodiverse ecosystem. Many of the destructive causes are already carefully studied and evaluated. However, knowledge about the more recently indicated destructive siltation process is still lacking and insufficient. The aim of this study was to try to understand siltation and its effect on mangroves, since this information can be used to indicate, protect and rehabilitate silted mangroves.

This master thesis starts with a short LITERATURE REVIEW, illustrating some basic background on mangroves, siltation, the studied species and the study area. This chapter ends with the enumeration of the research goals. In the following chapter, MATERIALS AND METHODS, a detailed explanation can be found of how this study was performed, how the study sites were divided, how data was collected/processed and which statistics have been used. The data and the statistical results of this research are presented in the RESULTS chapter and further discussed in the DISCUSSION chapter by proposing hypothesises and explanations. The last chapter, CONCLUSION AND PERSPECTIVES, gives a brief summary of the most important findings of this study followed by some suggestions for future research.

CHAPTER 1

1. Literature Review

1.1 Mangrove Ecosystems

1.1.1 Mangrove definition

Mangroves consist of a wide variety of tropical trees or woody shrublike plants growing at the interface between sea and land (intertidal zone), and form a highly productive and ecologically important ecosystem, often found in combination with coral reefs and seagrass beds (Tomlinson, 1986; Kathiresan *et al.*, 2001). Except for the most exposed or rockiest shorelines, they occupy all regions between mean sea level to highest spring tide in tropical and subtropical latitudes making these forests daily subjected to tidal changes in water height, salt concentration and temperature and corresponding varying degrees of anoxia (Alongi, 2008). Mangroves preferably settle in river deltas, estuarine complexes and lagoons (Thom, 1984), whereas they rarely settle in stagnant water (Gopal *et al.*, 1993). These ecosystems typically experience a low or average wave impact assuring no wash off of the muddy substrate, rich of organic material (Sternberg *et al.*, 2007).

The word 'mangroves' represents a non-taxonomic term which describes a diverse group of tropical plants that are well adapted for the life in a tidal, wet and saline habitat (Feller *et al.*, 1996). However, the term is not solely used to describe this unique ecosystem, it is also commonly used to refer to individual species living within the mangrove forest itself (Tomlinson, 1986). Hence, to avoid contextual confusion, the term 'mangal' or 'mangrove forest community' is used to refer to mangrove forests including their associated fungi, bacteria, flora and fauna (biotic factors) and the term 'mangrove ecosystem' is used to describe abiotic and biotic characteristics of mangrove forests (Macnae, 1968; Tomlinson, 1986; Kathiresan *et al.*, 2001).

Conform to the floristic limits of mangrove plants, Tomlinson (1994) defined tree groups: major mangrove elements, minor mangrove elements and mangrove associates. A species is considered as a major mangrove element (Table 1.1) when the following 5 assumptions are fulfilled. These assumptions are typical but not exclusive for mangrove species:

- The species are adapted to the stressful mangrove environment
- They have the ability to form pure (monospecific) stands and play a major role in the structure of the community.
- They are taxonomic isolated from their terrestrial relatives.
- Morphological specializations are present to adapt to their habitat (for instance pneumatophores, propagula,..)
- Physiological specializations are present as habitat adaptations (for instance salt exclusion, salt excretion,..)

True mangroves are evergreen and unique facultative woody halophytes (Komiyama *et al.*, 2008). Mangrove plants belong to the group of minor mangrove elements when they do not have the ability (most of the time) of forming conspicuous zones within the forest. They are mostly situated at the periphery of the mangroves (Tomlinson, 1986; Schmitz, 2004). The group of mangrove associates contains species that are never inhabitants of the strict mangrove community and are found in the transitional vegetation.

Table 1.1: An overview of the mangrove species belonging to the major mangrove elements (true mangroves) with an indication of the presence of aerial roots and vivipary, based on data of Tomlinson (1994) and updated with APG II (2003)(*) (De Ryck, 2009).

Family	Genus	# of mangrove species	Aerial roots	Vivipary
Acanthaceae*	*Avicennia*	8	++	+
Combretaceae	*Laguncularia*	1	+	-
	Lumnitzera	2	+	-
Palmae/Arecaceae	*Nypa*	1	-	+
Rhizophoraceae	*Bruguiera*	6	++	++
	Ceriops	2	++	++
	Kandelia	1	-	++
	Rhizophora	8	++	++
Lythraceae*	*Sonneratia*	5	++	-

++ present or well developed; + present; - absent

The mangroves contain 40 to 70 species belonging to a total of 16 families of dicotyledons and monocotyledons (Tomlinson, 1986; Feller *et al.*, 1996; Kathiresan *et al.*, 2001). According to Kathiresan *et al.*(2001), the major mangrove elements include 34 species of 5 families, whereas the minor mangrove elements include another 20 species belonging to 11 families.

1.1.2 Distribution

Mangroves are distributed globally in the intertidal zones of the tropical and subtropical regions located between 30°N and 30°S latitude (Tomlinson, 1986; Kathiresan *et al.*, 2001; Giri *et al.*, 2011), although Choudhury (1997) restricted this range to 25°N and 25°S. The habitats of mangrove forests are delimited by the major ocean currents and the 20°C-isotherm of seawater during the yearly coldest period (Alongi, 2002). The highest percentage of mangroves are situated between 5°N and 5°S latitude (Giri *et al.*, 2011) (Fig 1.1).

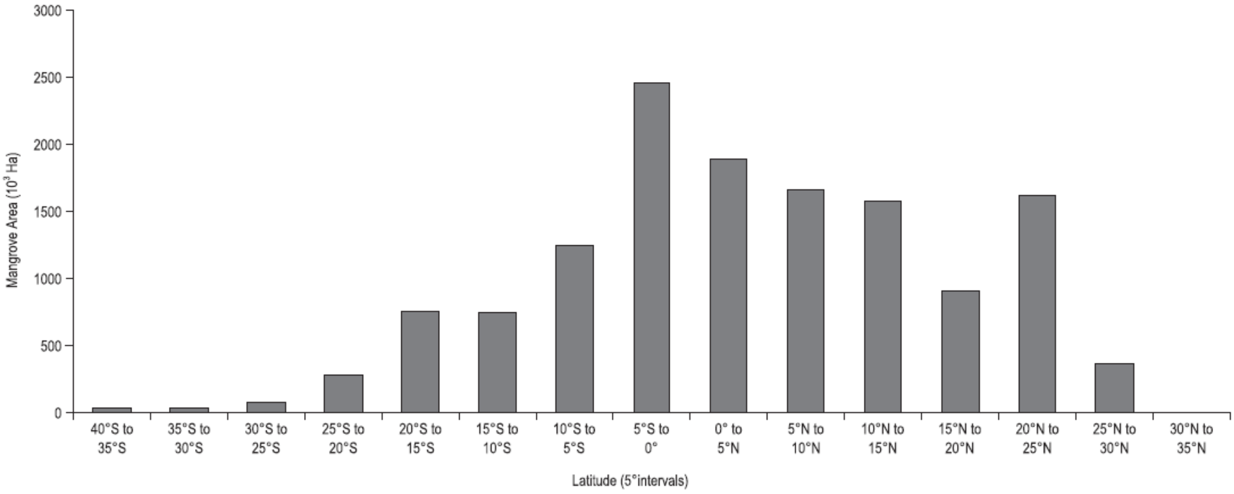


Figure 1.1: Latitudinal distribution of mangroves over the world in latitude intervals of 5° (Giri *et al.,* 2011).

The total area that is covered by mangrove forests is estimated at 110.000 up to 240.000 km² (Fig 1.2), this large range results from poor measuring techniques used for area estimation and measurement. Giri *et al.* (2011), who made the most comprehensive mapping study ever based on a 30-m spatial resolution, estimated the mangrove area of the year 2000 at 137.760 km² (Fig 1.3) which was located in 118 countries and covered 0.7% of all tropical forests in the world. Unfortunately, this current estimate is less than half of what it once was (Spalding *et al.*, 1997; Finlayson *et al.*, 1999) and what is left of this area is mostly in degraded conditions (Giri *et al.*, 2011). According to Alongi *et al.* (2002), one third of the world's mangrove forests has been lost in the last 50 years. Yet, still no more than 6.9% of this unique ecosystem is currently protected (Giri *et al.*, 2011)

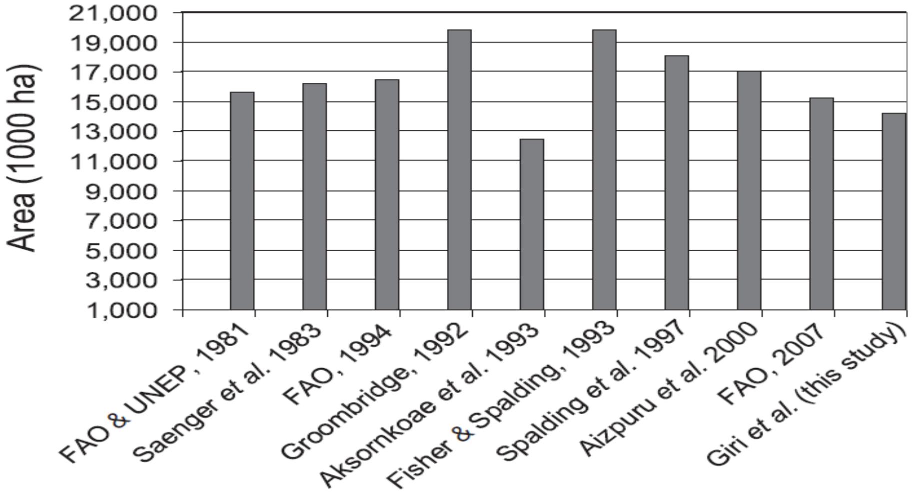
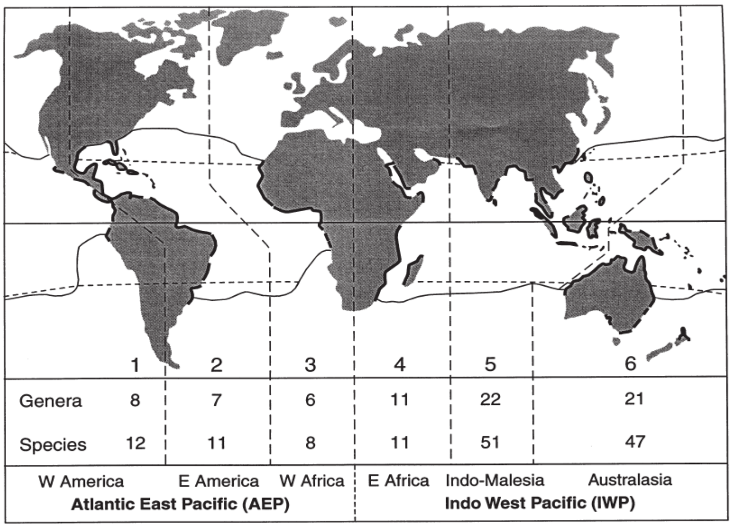


Figure 1.2: Different studys trying to estimate the area covered by mangroves with their respective estimated amount (Giri *et al.,* 2011).

Figure 1.3: Mangrove distribution in the world. Mangrove areas are indicated with black markings (Giri *et al.*, 2011).

When looking for the total amount of mangroves per continent, Asia has the highest percentage of the worldwide mangrove area (42%), followed by Africa (20%) and North and Central America (15%). Oceania and South America both attribute for respective 12% and 11% to the total amount of mangrove forests. In Europe, no mangroves will be found since environmental conditions are not suitable for the survival and settling of these trees.

When studying all mangrove areas and species worldwide, 2 main distinct bio-geographic regions of mangroves are distinguished (Walsh *et al.*, 1974; Alongi, 2002) (Fig 1.4). The first region with the lowest amount of genera and species is known as the Atlantic East Pacific (AEP) and overlaps with the American continent and the whole western part of Africa. However, more genera and species of mangrove trees can be found in the second region, the Indo West Pacific (IWP) region, containing the eastern part of Africa, Indo-Malaysia and Australia.



	1	2	3	4	5	6
Genera	8	7	6	11	22	21
Species	12	11	8	11	51	47
	W America	E America	W Africa	E Africa	Indo-Malesia	Australasia
	Atlantic East Pacific (AEP)			Indo West Pacific (IWP)		

Figure 1.4: Number of genera and species per land zone of to the two bio-geographical regions of mangroves, the Atlantic East Pacific (AEP) and the Indo West Pacific (IWP) (Alongi, 2002).

1.1.3 Cause of distribution

Although mangroves are globally spread, they require the presence of a certain number of biotic and abiotic characteristics before they can settle in a certain region (Macnae, 1968; Walsh *et al.*, 1974; Pool *et al.*, 1977; Ruwa *et al.*, 1986; Tomlinson, 1986; Kathiresan *et al.*, 2001). These requirements can therefore explain the distribution of these forests.

1.1.3.1 Climate

Waisel *et al.* (1972) and Walsh *et al.* (1974) noticed that tropical species, including mangroves, do not satisfactorily develop when annual average temperatures are below 19°C, which approximately corresponds with the sea water isotherm of 20°C during the coldest period of the year (Alongi, 2002). Since mangrove trees are intolerant to freezing temperatures both air and water temperatures may never decrase below 0°C (Waisel, 1972; Sherrod *et al.*, 1985; Sherrod *et al.*, 1986; Tomlinson, 1986). Optimal temperatures for mangroves are not only limited by cold temperatures, but also by high temperatures because they hinder the tree settling. Photosynthesis of most mangrove species sharply declines when the air temperatures exceeds 35°C and is even reduced to zero when the thermal compensation point of 39°C is reached (Moore *et al.*, 1972; Moore *et al.*, 1973). Exposure of seedlings of *Avicennia* to water temperatures higher than 40°C for a period of 48h results in high seedling mortality (McMillan, 1971). As such, it seems that the temperature of both water and air are important regulators of the presence or absence of mangroves. In addition, the amount of rainfall is an important feature influencing tree settling. Macnae (1968) indicates the preference of mangroves for regions where a relatively high input of rainfall is assured.

1.1.3.2 Tidal inundation, wave energy and salinity

It is commonly accepted that mangroves do not depend on the tidal of salt seawater for their growth and existence since they are no obligated halophytes. Several scientists (Tomlinson, 1986; Ball, 1988a) noted the possibility for these trees to grow under fresh water conditions, where salinity is low. It is not the direct effect of flooding by the tides and salinity that provides ideal growth conditions for the trees, but the indirect effects of these parameters causing a decline of the competitive force of other vascular plants. The high salinity and anoxic conditions associated with the flooding increase the competitive advantage of mangrove tree species (Sternberg *et al.*, 1987).

Tomlinson (1994) provided a division according to the frequency of inundation of certain regions within a mangrove forest, by the tides. The distinction in five classes (Table 1.2) was based on the frequency of becoming waterlogged by the tides, which is mostly linked with the distance towards the ocean. Inundation class 5 corresponds with the area that gets flooded by the tides only during the equinoxes (spring and neap tide).

Table 1.2: Inundation classes and their respective frequency of inundation according to Tomlinson (1986).

Inundation class	Inundation frequency (%)
1	100 - 76
2	75 - 51
3	50 -26
4	25 - 5
5	< 5

1.1.3.3 Substrate characteristics

The substrate of mangrove forests forms a typical characteristic for these ecosystems since it consists of a fine-grained mud of silt and clay containing large quantities of organic matter and only a low amount of nutrients and oxygen due to depletion by respiration of aerobic soil bacteria (Hogarth, 2007). These properties again result in a competitive advantage of mangrove trees compared with other vascular plants. The soil can contain sometimes high amounts of sulphur, which has a negative impact for plants and tree, including mangrove trees. Salt water input by the tides controls these amounts assuring bearable concentrations for the mangrove trees.

Big waves with strong wave action are not preferred, since they will transport the typical mangrove sediment and the seedlings outwards the mangrove causing a decline in settling of seedlings and disappearance of the favourable underground. Mangroves are therefore found in more protected coastal areas (Tomlinson, 1986).

Small topographic gradients are in favour of mangrove forests because they produce a larger tidal area (Srivastava *et al.*, 2012). As such, it is no exception to find mangroves adjacent to estuaries and large rivers, such as the Ganges in Bangladesh, the Fly river in Papua New Guinea and the Mekong Delta in Vietnam.

1.1.4 Spatial pattern of mangrove zones

Many scientists (Davis, 1940; Macnae, 1968; Lugo *et al.*, 1974; Chapman, 1976; Feller *et al.*, 1996; Sorrell *et al.*, 2000; Krauss *et al.*, 2008) describe a distinct spatial pattern in the appearance of mangroves all over the world (Matthijs *et al.*, 1999), containing different species from monospecific patches or bands of vegetation parallel to the shoreline. Currently, scientists are still debating the underlying cause creating these distinct spatial zones. Davis (1940) related these zones to the succession pattern of different species, however, his hypothesis is no longer accepted by other scientists. Other hypotheses explaining the zonal pattern are related to: (1) the geomorphic processes (Thom, 1967), (2) the physical ‘sorting out’ of the propagules by the tidal action across a certain gradient, also referred to as dispersal dynamics (Rabinowitz, 1978), (3) the physiological tolerance of the species for water logging and salinity (Clarke *et al.*, 1970; Jimenez *et al.*, 1991), (4) the succession caused by competition between different species (Ball, 1980), (5) the predation of the propagules (Smith, 1987), and (6) the physiological specializations allowing species only to grow where these physiochemical conditions are met (Ball, 1988b; McKee, 1995), such as soil redox potential (Eh) (Boto *et al.*, 1984) and water sulphide concentrations (Nickerson *et al.*, 1985; McKee, 1993).

1.1.5 Adaptations to extreme environmental conditions

1.1.5.1 Salt

Mangroves are facultative halophytes, meaning that they do not need the presence of salt but it is profitable. Therefore they can still grow and function well even up to a salinity of 90 particles per thousand (ppt = g/l), but they perform the best when salinity fluctuates between 5 and 75 ppt (Krauss *et al.*, 2008). The diurnal fluctuations of salt concentrations accumulating in the rhizosphere are caused by the tides bringing seawater (35ppt) into the mangroves (Parida *et al.*, 2010). This extreme variable forces mangrove trees to adapt to assure water uptake from the sea water which has an osmotic water potential of -2.5MPa (Hogarth, 2007) and to avoid salt entering the tree. Therefore, water potentials created over the tree have to be lower than -2.5MPa, making water uptake and distribution through the whole tree possible (Scholander *et al.*, 1964) since water flows from a higher to a lower water potential (Steppe, 2011).

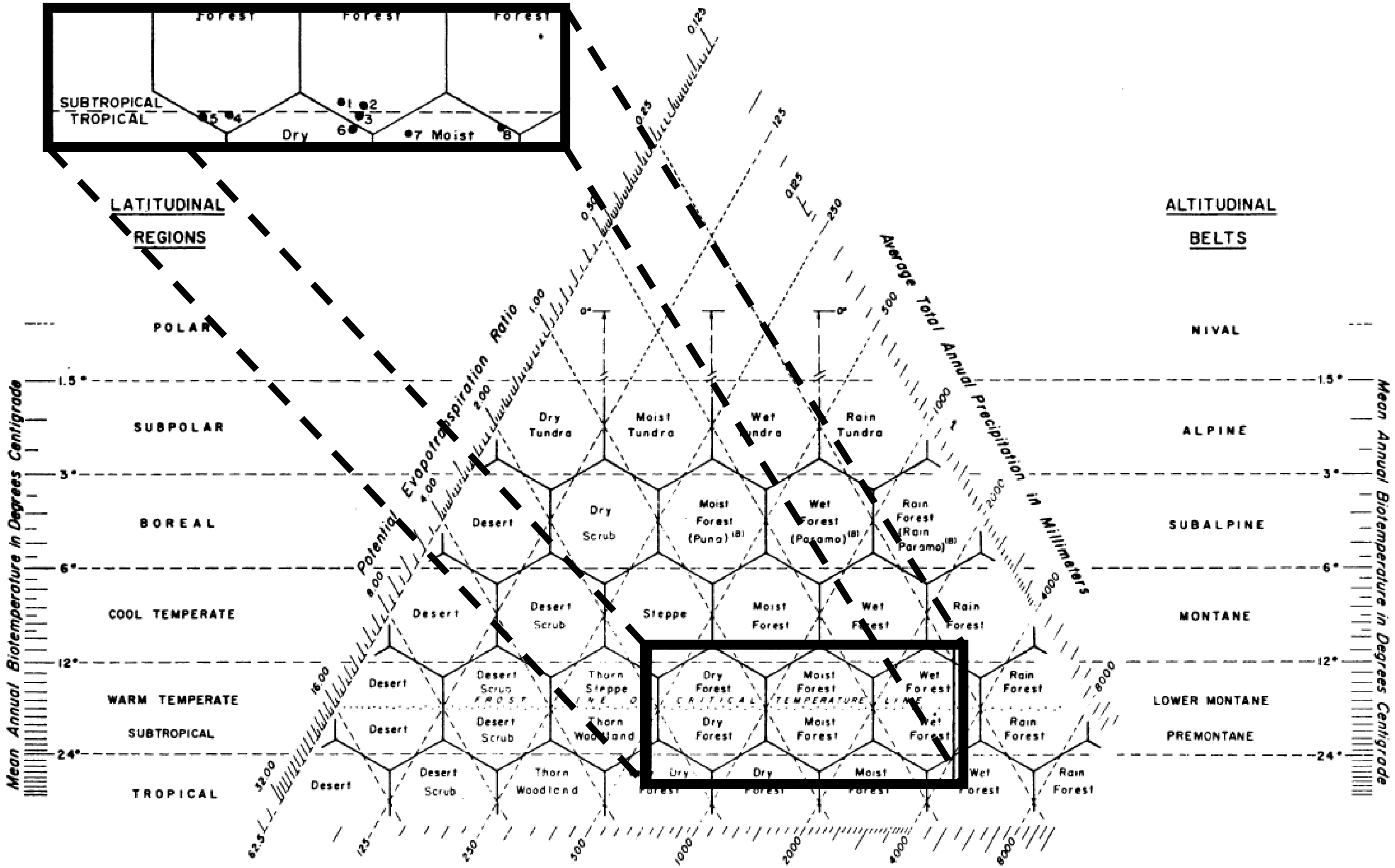


Figure 1.5: Diagram for the classification of world life zones or plant formations by L.R. Holdrigde (1967), where 8 different American mangrove regions are indicated using available climatic data. Result shows the presence of studied mangroves are located in the subtropical and tropical dry and moist life zones. (1) Ten Thousand Islands, Florida; (2) Turkey point, Florida; (3) North Coast, Puerto Rico; (4) South Coast, Puerto Rico; (5) West Coast, Mexico; (6) Santa Rosa, Costa Rica; (7) Boca Borranca, Costa Rica; (8) Moin, Costa Rica. (Pool *et al.*, 1977)

Since mangrove plants have no salt resistant metabolism (Ball *et al.*, 1986), they are adapted with some physiological mechanisms to exclude or excrete salt (Drennan *et al.*, 1982). The salt concentration within sap of different mangrove species ranged from 0.5 ppt up to a maximum of 8 ppt found in *Avicennia* (Scholand *et al.*, 1966) which is much lower than the salinity of sea water and indicates adaptations against the high salinity of the sea water.

Mangrove plants can be subdivided in two groups according to their ability to regulate salt concentrations and to achieve a certain degree of salt tolerance. The plants of the first group achieve salt regulations by the following physiological mechanisms: (1) salt exclusion by ultra-filtration at root level driven by the pulling force generated by transpiration (Scholander *et al.*, 1962; Tomlinson, 1986), (2) salt excretion by cuticular transpiration or by the use of salt glands positioned at the underside of the leaves (Fig 1.6). Both mechanisms are associated with relatively high NaCl concentrations in the xylem sap. (3) Salt accumulation within leaf cells followed by defoliation to remove the stored salt. The plants of the second group contain compatible, organic, cytoplasmic solutes ensuring osmoregulation and making them more salt tolerant (Popp *et al.*, 1993).

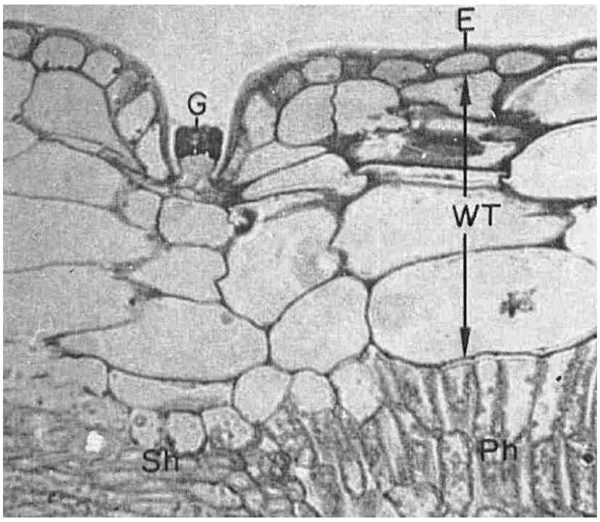


Figure 1.6: Cross section through a well-developed leaf. E: Adaxial epidermis; G: Salt gland; Ph: Photosynthetic tissue; Sh: Bundel sheath cell; WT: Water tissue (Shimony *et al*., 1973).

1.1.5.2 High temperatures and high relative humidity

Some adaptations of mangrove species to avoid too much water loss due to transpiration are thick leaves with waxy cuticula, the presence of small hairs on the leaves, good regulation of stomata and the storage of water within the leaves.

1.1.5.3 Soil characteristics

Typical mangrove soils consist of a muddy composition of silt and clay, which have a high content of organic matter due to the fast decomposition of the leaves within this ecosystem (Ashton *et al.*, 1999).

However, these soils are depleted of nutrients (assuming no human interference) and water logging and activity of aerobic bacteria result in anaerobic conditions causing a black colour. Only the surface layers are oxidised (Macnae, 1968; Boto *et al.*, 1984), as such the trees require appropriate mechanisms for oxygen uptake. Pneumatophores or aerial roots, which are above-ground rootlike structures containing lenticels and aerenchyma tissue (Fig 1.7), form a pathway for gas exchange from the atmosphere to the underground roots (Scholander *et al.*, 1955; Macnae, 1968; Walsh *et al.*, 1974). Roots have the urge to strongly develop in a horizontal plane, near the surface to assure the plants stability and anchorage.

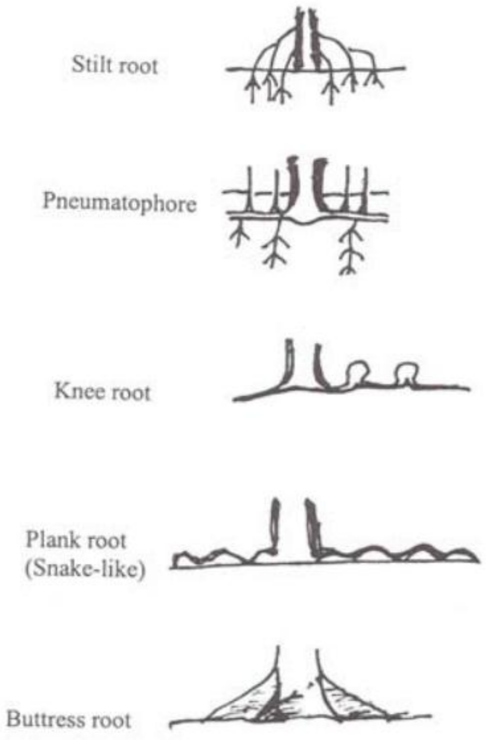


Figure 1.7: The different forms of aerial roots found for mangrove species (Kathiresan *et al.*, 2001).

1.1.5.4 Reproduction

Mangrove forests have little capacity for vegetative propagation, thus the forest depends for its maintenance and spread on the seedlings (Tomlinson, 1986). The reproduction and distribution of mangrove tree species is based on vivipary and hydrochory (Rabinowitz, 1978; Tomlinson, 1986; Tomlinson *et al.*, 2000). Vivipary is a form of reproduction where the embryo of the seed continues its development without a period of dormancy, resulting into a seedling which is still attached to the parent plant (Carey, 1934; Elmqvist *et al.*, 1996). When the diaspora (Fig 1.8), also known as seedling or propagule, are dropped from the tree, tidal action will provide the capacity for dispersal. Distribution using water as a carrier medium is known as hydrochory. To assure the floating capacity of the seedlings, propagules are accommodated with an aerenchymatic cortex within the hypocotyl (Macnae, 1968; Tomlinson *et al.*, 2000).

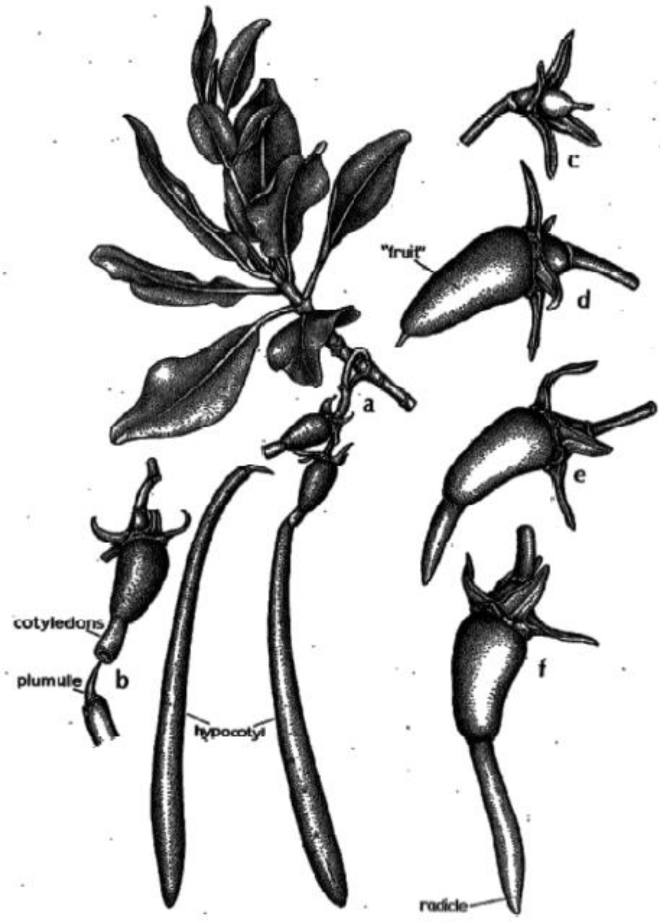


Figure 1.8: Developmental and growth stages of the propagule belonging to the mangrove species *Rhizophora mangle* (Tomlinson, 1986).

1.1.6 The benefits of mangroves

Unfortunately, the many positive influences and high values linked to the mangrove ecosystem are today often ignored. The most important benefits of this ecosystem are listed below:

- Protection barrier against storms, hurricanes and tsunamis (Tri *et al.*, 1998; Alongi, 2008).
- Sediment filter and trap for suspended solids assuring filtering of the upland runoff, protecting the coral reefs and sea grass beds for the negative effect of suspended particles (Fig 1.9).
- Avoidance of coast erosion (Alongi, 2008).
- Provides a nursery ground for many fish species (Nagelkerken *et al.*, 2000)
- Counteract global heating by its high amount of carbon sequestration (Giri *et al.*, 2011).
- Mangroves are considered as a supplier of natural products such as charcoal, wild honey, timber, food and medicinal element (Dahdouh-Guebas *et al.*, 2000).

- Supporting a high abundant and diverse variety of wildlife, including some endangered species (Moberg *et al.*, 2003).
- Tourism, aesthetical, cultural and spiritual value.

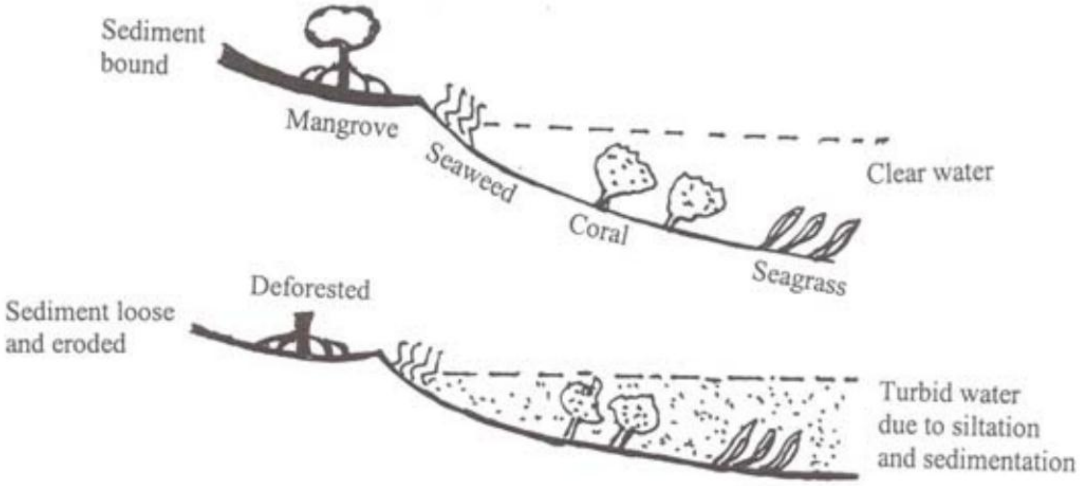


Figure 1.9: The effect of deforestation of mangroves, resulting in turbid water and the degradation of coral reefs and sea grass beds (Kathiresan, 2011).

1.1.7 Threats for mangrove ecosystems

A sever and large-scale decline in mangrove area took place during the past century. Duke *et al.* (2007) estimated this disappearing rate up to 2% per year, which even goes beyond the degradation rate of coral reefs and tropical rainforest. During the last quarter of the century, 35% to 86% of the mangrove ecosystems disappeared, making the remaining forests smaller and more fragmented. The long-term survival of this ecosystem is therefore at great risk as estimations based on current degradation rate indicate that all mangroves will be lost during the next 100 years (Duke *et al.*, 2007). This high destruction rate of mangrove ecosystems is related to their high sensitivity for disturbance since they live close to the tolerance limit (Kathiresan *et al.*, 2001).

The destruction mostly originates from human interference: (1) the mangrove ecosystem is often seen as endless source for services and goods (De Ryck, 2009), and (2) the lack of responsibility that seems to go along with common goods, also called the tragedy of ‘commons’ (Hardin, 1968). Some of the major causes and future threats of mangroves are listed in Table 1.3. Therefore, an answer on the urgent and increasing demand for more investments in the preservation of this ecosystem, has to be found by this and next generation.

“*Ecological morality is a luxury that poor and underprivileged people don’t have.*”

(By Swertvaegher J.; 2012)

This quote indicates the complexity that goes together with ecological management and nature conservation. One of the most important causes of mangrove degradation lies in the attempt of people to fulfil in their basic life supports and those of their families. Sensitizing and involving the local people has to be a priority in conservation to guarantee success.

Table 1.3: Present and future threats

Present and future threats	References
Clear cutting for timber and charcoal	(Mohamed *et al.*, 2009)
Hydrological alterations	(Blasco *et al.*, 2001)
Agricultural land change and nutrient increase	(Giri *et al.*, 2011)
Urban development and housing	(Abuodha *et al.*, 2001)
Pollution and oil spill	(Abuodha *et al.*, 2001)
Siltation	(Ellison, 1998)
Aquaculture and shrimp ponds	(Vaiphasa *et al.*, 2007)
Sea water rising and global warming	(Gilman *et al.*, 2008)

1.2 Siltation

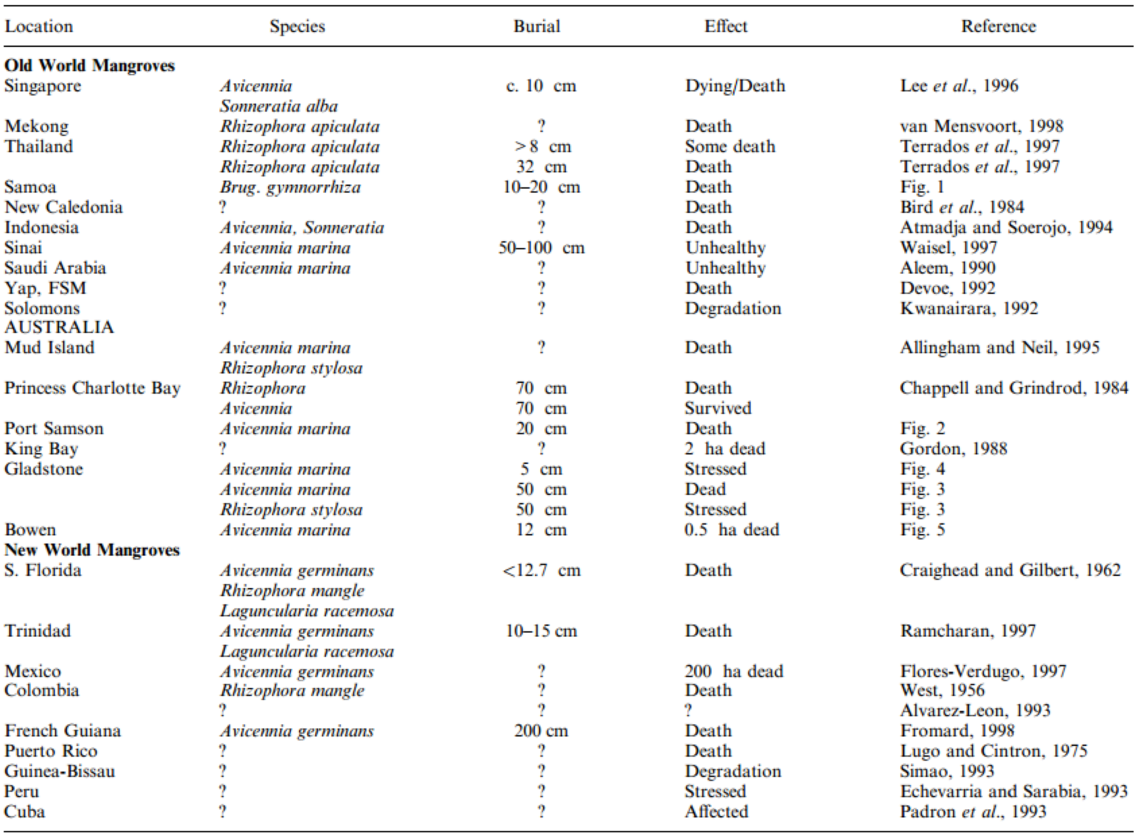
1.2.1 Definition of siltation

Sedimentation is defined as the natural, slow process of settling out suspended solids in water towards the substrate. In addition, sedimentation causes land forming and does not result in any additional negative effects on the trees. 'Siltation', on the other hand, indicates an unusually high increase of the sedimentation rate, mostly implying negative effects and, hence, abiotic stress for the trees. Siltation is often caused by human interference which causes the natural sedimentation rate to increase.

Sedimentation is a natural process of which an increase in sediment on the former top layer is established. A mangrove forest is subjected to sedimentation when the sedimentation rate is higher than the erosion rate and thus causing an increase in the thickness of the upper soil layer. This process is known to be typical for mangrove ecosystems where it assures an indispensable import of nutrients. Mangroves function naturally as sediment sinks where suspended solids are filtered out of the water resulting in a positive effect on the associated coral reefs and sea grass beds laying off shore. However, for this reason, mangroves are in particular more sensitive for siltation, because negative effects on plant performance arise when suspended solids accumulated too fast in the mangrove ecosystem.

Moderate sedimentation rates can be positive for mangroves leading to enhanced growth of the trees (Ellison *et al.*, 1996; Pezeshki *et al.*, 1997; Ellis *et al.*, 2004). This phenomenon can be explained by the higher availability of nutrients which comes together with the newly formed soil layer (Alongi *et al.*, 2005). In particular, the enhanced phosphor availability would be beneficial for the growth of mangrove trees (Nye *et al.*, 1977). However, high sedimentation rates which exceed 1 cm year^{-1}, would cause a seriously dieback and high death ratio within the mangrove forests (Ellison et al., 1998). This was strengthened by many studies, all indicating the negative influence of siltation. Vaiphasa *et al.* (2007), for instance, found a significant lower growth rate for mature mangrove trees and a total absence of colonization by seedlings within study sites that were silted. Other observations indicated the loss of 100 ha of mangrove ecosystems by the deposit of dredged-up sediment originating from the Mokowe Sea Jet construction in Kenya (Abuodha *et al.*, 2001). All over the world, research pointed out that siltation forms a direct cause for the loss of mature mangrove trees (Table 1.4) (Lugo *et al.*, 1975; Hutchings *et al.*, 1987; Gordon, 1988; Ellison *et al.*, 1996; van Mensvoort, 1998; Vaiphasa *et al.*, 2007). Unfortunately, not only mature trees are negatively influenced, but also their seedlings encounter many problems and die due to siltation. This disturbs the life cycle of mangrove trees which leads to a faster decline of the forests and makes rehabilitation more difficult.

Table 1.4: Observations of silted mangrove over the whole world and their effects (Ellison, 1998).



Location	Species	Burial	Effect	Reference
Old World Mangroves				
Singapore	*Avicennia*	c. 10 cm	Dying/Death	Lee *et al.*, 1996
	Sonneratia alba			
Mekong	*Rhizophora apiculata*	?	Death	van Mensvoort, 1998
Thailand	*Rhizophora apiculata*	>8 cm	Some death	Terrados *et al.*, 1997
	Rhizophora apiculata	32 cm	Death	Terrados *et al.*, 1997
Samoa	*Brug. gymnorrhiza*	10–20 cm	Death	Fig. 1
New Caledonia	?	?	Death	Bird *et al.*, 1984
Indonesia	*Avicennia, Sonneratia*	?	Death	Atmadja and Soerojo, 1994
Sinai	*Avicennia marina*	50–100 cm	Unhealthy	Waisel, 1997
Saudi Arabia	*Avicennia marina*	?	Unhealthy	Aleem, 1990
Yap, FSM	?	?	Death	Devoe, 1992
Solomons	?	?	Degradation	Kwanairara, 1992
AUSTRALIA				
Mud Island	*Avicennia marina*	?	Death	Allingham and Neil, 1995
	Rhizophora stylosa			
Princess Charlotte Bay	*Rhizophora*	70 cm	Death	Chappell and Grindrod, 1984
	Avicennia	70 cm	Survived	
Port Samson	*Avicennia marina*	20 cm	Death	Fig. 2
King Bay	?	?	2 ha dead	Gordon, 1988
Gladstone	*Avicennia marina*	5 cm	Stressed	Fig. 4
	Avicennia marina	50 cm	Dead	Fig. 3
	Rhizophora stylosa	50 cm	Stressed	Fig. 3
Bowen	*Avicennia marina*	12 cm	0.5 ha dead	Fig. 5
New World Mangroves				
S. Florida	*Avicennia germinans*	<12.7 cm	Death	Craighead and Gilbert, 1962
	Rhizophora mangle			
	Laguncularia racemosa			
Trinidad	*Avicennia germinans*	10–15 cm	Death	Ramcharan, 1997
	Laguncularia racemosa			
Mexico	*Avicennia germinans*	?	200 ha dead	Flores-Verdugo, 1997
Colombia	*Rhizophora mangle*	?	Death	West, 1956
	?	?	?	Alvarez-Leon, 1993
French Guiana	*Avicennia germinans*	200 cm	Death	Fromard, 1998
Puerto Rico	?	?	Death	Lugo and Cintron, 1975
Guinea-Bissau	?	?	Degradation	Simao, 1993
Peru	?	?	Stressed	Echevarria and Sarabia, 1993
Cuba	?	?	Affected	Padron *et al.*, 1993

1.2.2 Origin of siltation events

Scientific reports (Thom, 1967; Ellison, 1998; Vaiphasa *et al.*, 2007) accumulate evidence pointing out the negative influence of siltation on mangroves trees caused by natural and/or anthropogenic processes, such as flush floods and tsunamis, waste discharges of shrimp ponds (Vaiphasa *et al.*, 2007) or sediment runoff and erosion due to land changes. The latter gains importance when soil vegetation and land use changes to a more favourable landscape for human activities (Hollins *et al.*, 2011). As climate change becomes more and more significant, the frequency of flush floods and tsunamis will increase (Mimura *et al.*, 2011) causing an increased sedimentation rate in the affected areas. Human interventions like channel forming, cutting of coast vegetation, destruction of coral reefs and sandbanks will enhance the inland tsunamis and the corresponding siltation.

Aquaculture and in particular the shrimp ponds, form a serious danger for mangroves (Fig 1.10). Not only trees are cut down for digging ponds, but also the dredged substrate is frequently discharged into the mangroves (Thom, 1967; Gautier *et al.*, 2001) leading to dieback of the forests. Research indicates that mangroves can withstand the chemical content of the shrimp farm wastes (Sansanayuth *et al.*, 1996; Chu *et al.*, 1998; Gautier *et al.*, 2001) and even can act as a purifying filter (Tam *et al.*, 1995; Gautier *et al.*, 2001). The cause of the decline in mangrove area can therefore be assigned to the sudden high sedimentation rate leading to a silted ecosystem.

Figure 1.10: Mangrove destruction by shrimp ponds

The sediments and suspended solids that are dropped in the mangroves causing the siltation, can originate from inland regions or from the seas or oceans. When higher percentages of fine sand are found as deposit, this would suggest that the siltation originates from marine sediments which were re-suspension by the wind-wave energy (Ellis *et al.*, 2004). Higher degrees of silt and clay would indicate that the sediments originate from inland regions. Burial by sand results in lower dieback rate of the trees compared with areas covered by silt and clay as siltation (Vaiphasa *et al.*, 2007). This is probably due to the better aeration in a sandier top layer.

1.2.3 Anatomical and physiological impact of sedimentation

It is not yet fully clear what in particularly causes the negative siltation effect on trees. The most important cause is probably that roots and pneumatophores are getting smothered by siltation resulting in oxygen stress (Ellison, 1998). Root damage and oxygen deficiency are caused by the inhibition of the gas exchange pathway between atmosphere, roots and soil (Ellison, 1998; Abuodha *et al.*, 2001; Thampanya *et al.*, 2002). This hypothesis is strengthened by observations that trees with partly covered pneumatophores exhibit an enormous oxygen stress and die when the pneumatophores are fully covered (Allingham *et al.*, 1995). *Rhizophora* trees seem at first sight less subjected to siltation due to their large amount of stilt roots, which appears less susceptible for forming a smothering layer of sediment and leave as such large root parts still capable of aeration. However, this species turned out equally sensitive for siltation, probably their lenticels are positioned just above the substrate and are easily disturbed by the formation of a smothering layer (Terrados *et al.*, 1997).

Vaiphasa *et al.* (2007) pointed out that a serious disruption of the tidal pattern can occur due to siltation, which can change the physicochemical characteristics of the substrate, e.g. an increase of salinity. This creates less favourable conditions for mangrove trees and can result in the decline of mangrove forests.

1.3Avicennia marina and *Rhizophora mucronata*

1.3.1 Classification

The family of Avicenniaceae contains 8 (10 according to classification) different species of which one is characterised by small sized yellow to orange flowers (Fig 1.11,a) and is known as *Avicennia marina* (Forsk.) Vierh. (Tomlinson, 1986). This species is also commonly addressed as the grey mangrove tree. *Avicennia marina* is a pioneer species and thus can cope with more unfavourable conditions compared with other mangrove trees. This also explains that *Avicennia* has the broadest distribution and is one of the most abundant species in mangrove forests. Exceptional is the double distribution of this species, meaning that *Avicennia marina* is found dominant within both the lowest and highest intertidal zone, but rarely seen or even absent in the middle intertidal zone. Their size can vary from small shrubs and dwarf trees up to 30 meters high trees.

Figure 1.11: Morphology of *Avicennia marina*: (a) inflorecense (©Murray P.), (b) pen roots (©Steyn P.) and (c) germinating propagule (©Lawler W.)

The family of Rhizophoraceae is subdivided in 15 genera, which contains together around 140 species (Schwarzbach *et al.*, 2000). Flowers can be recognised by their yellow-white calyx with 4 thick and hard calyx lobes, alternating with the 4 hairy and white petals. Typical cork warts are positioned at the underside of the leaves. This species is mostly found as a monospecific dens patch of trees adjacent to water. *Rhizophora* trees can form shrubs, which will gradually increase in height, up to 20m, when approaching the ocean, sea or river.

Both these species are classified as C3 plants since CO_2 is fixated by the use of intermediates which contain 3 carbon atoms. These 3 carbon atoms are converted into glucose ($C_6H_{12}O_6$) using light energy. For more details on this process, we refer to (Taiz *et al.*, 2006; Steppe, 2011).

1.3.2 Adaptation to cope with high salinity

Avicennia marina has the ability to exclude and excrete salt. At root level, microfiltration will assure that at most 10% of the salinity of sea water will be found in the sap of the tree. Due to the presence of salt glands on the leaves, the excess of salt can be secreted (Parida *et al.*, 2010) (Fig 1.6). *Rhizophora marina* lacks salt glands, but has a more strict salt exclusion at root level, avoiding salt entering the sap of the tree.

1.3.3 Wood anatomy

The wood anatomy of *Avicennia* is characterized by anomalous uniform growth rings which are however not correlated with the age of the tree (Robert *et al.*, 2011b). Each ring consists of a band of xylem containing vessels and a band of conjunctive phloem tissue (Tomlinson, 1986). Between the parenchyma layers, successive cambia can be found. According to Robert *et al.* (2011), the intricate non-concentric three dimensional network of phloem and xylem tissue within *Avicennia marina* assured a better linkage for water transport within the tree. In contrast, annual growth rings are present in *Rhizophora mucronata*, creating the possibility of dendrochronology and dendrochemistry (Verheyden *et al.*, 2004; Verheyden *et al.*, 2005).

Avicennia marina has typical negatively geotropic pencil like pneumatophores with a size mostly smaller than 30 cm(Tomlinson, 1986), in this research indicated as pen roots (Fig 1.11,b). *Rhizophora mucronata* forms a cluster of aerial stilt roots.

1.3.4 Reproduction

Cryptovivipary is a typical form of vivipary found for the very short-beaked, bean-like fruits of *Avicennia* species (Fig 1.11,c), but is also found for *Aegialitis*, *Aegiceras*, *Laguncularia*, *Nypa* and *Pelliciera* species. Cryptovivipary originates from the Greek word *kryptos* which means hidden and it refers to the condition whereby the embryo grows within the fruit resulting in the rupture of the seed coat. However, it will not enlarge sufficiently for breaking through the fruit wall before it splits open (Saenger, 2002). On the other hand, *Rhizophora mucronata* has a characteristic propagule with a long shaped hypocotyl becoming narrower at the top and which can reach a length of 70 cm (Fig 1.8). When dropped from the parental tree, it can directly spears in the muddy soil or it can be carried away by the tides.

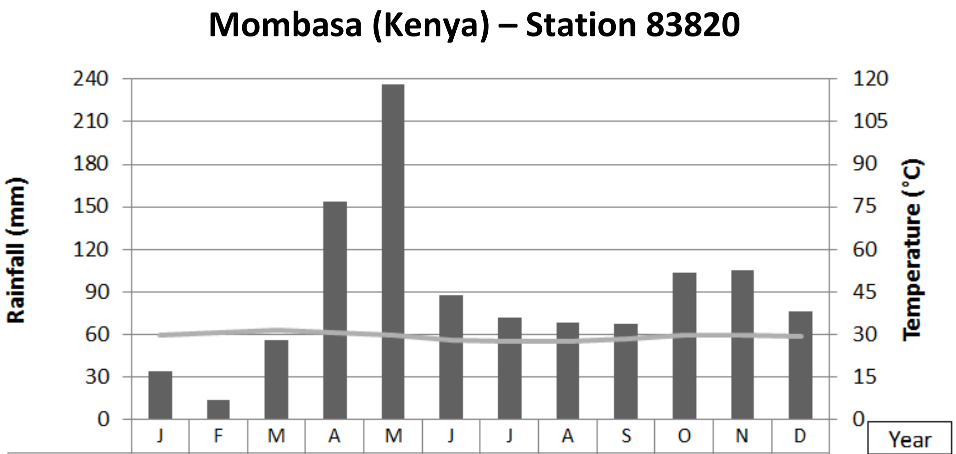
1.4Study area description and research goals

1.4.1 Selection study site

The mangrove forest of Mikindani (S 04°00’; E 039°38’), located in the suburbs of Mombasa (Kenya), was chosen as the study area (discussed in chapter 2). A motivation for this choice was that due to landuse change (human encroachment) on the slopes surrounding this area, the mangroves of Mikindani (Tudor Creek) were subjected to siltation, causing the degradation of the local mangrove vegetation (Mohamed *et al.*, 2009). In addition, the heavy rains in the year 1997 owing to the ENSO (El Niño Southern Oscillation) caused a flush flood, bringing along marine sediment into the mangroves, resulting in a silted subsoil.

1.4.2 Climate

Mombasa and the surrounding regions are subjected to a warm and tropical climate. The semi-annual passage of the inter-tropical convergence zone (ITCZ) and the monsoons are causing an alternation of rainy and dry periods, resulting in two rainy and two dry seasons a year. The wettest period occurs first during the months of April and May, while the second, less pronounced, rainy period takes place in October and November (Fig 1.12). January and February are known as the driest months on yearly basis. Annual temperature fluctuations are insignificant, varying even less than the diurnal temperature fluctuations, as much the terms of a hot or dry period cannot be used here. The total annual rainfall is around 1073 mm/year and the annual temperature reaches an average of 29.3°C (Fig 1.12). However, one has to bear in mind that reality can differ from this pattern.



	J	F	M	A	M	J	J	A	S	O	N	D	Year
▬ R (mm)	34	14	56	154	236	88	72	68	67	103	105	76	1073
▬ T (°C)	29,7	30,6	31,4	30,7	29,6	27,9	27,4	27,6	28,4	29,7	29,9	29,2	29,3

Figure 1.12: Climatological information of Mombasa, average from 1961 up to 1999. This figure is based on collected data by Lieth (1999) and employees of RMI Belgium.

1.4.3 Study goals

The aim of this research is to find the answer on the following research questions:

(1) Does siltation have a negative influence on the performance of *Avicennia marina* and *Rhizophora mucronata* trees?

(2) How are anatomical and hydraulic features of *Avicennia marina* and *Rhizophora mucronata* trees influenced by sedimentation?

Trees will be studied under natural conditions, in two sites of different relative siltation level, in a mangrove forest near Mombasa (Kenya). *Avicennia marina* and *Rhizophora mucronata*, which are two abundant mangrove species with a worldwide spread, have been studied during this research.

Studying both the stomatal conductance and the hydraulic conductance between sites which are subjected to a different degree in siltation would indicate if siltation indeed has a negative influence on one or both mangrove species. One can expect the values for both parameters to be lower when a tree becomes stressed.

The study of anatomical and hydraulic features is interesting since trees will change these properties in an attempt to cope with less favourable environmental conditions. Besides, these features influence the

the stomatal conductance and the hydraulic conductance and thus would give valuable information about the underlying physiological reason of the resulting values for both stomatal conductance and hydraulic conductance.

At the end of this research, a more detailed and coherent picture will be formed on the effect of siltation on *Avicennia marina* and *Rhizophora mucronata* and how these species attempt to counteract this siltation. Since the vast decline of mangrove forest and the need for better preservation of this ecosystem are contemporary concerns, results of this study can give valuable knowledge for faster detection, counter action and rehabilitation of silted mangroves.

CHAPTER 2

2 Material and Methods

2.1 Study site and measurement period

The study area was divided into several sites for observation and measurement(Fig 2.1). Site distinction has been made based on siltation and the species difference. This distinction resulted in four sites, two low siltation sites with a low level of siltation, one with *Avicennia marina* Forssk. Vierh (AL) and one with *Rhizophora mucronata* Lam. (RL), and two high siltation sites with a high level of siltation, again one with *Avicennia marina* (AH) and one with *Rhizophora mucronata*. (RH). All four sites were situated in inundation class four, which is flooded twice a day (according to the oceanic tides) by sea water (35 ppt). Fresh water input mostly originates from direct rainfall and ensuing run-off. Sampling took place in between both rainy periods, from 10 July until 15 August 2011.

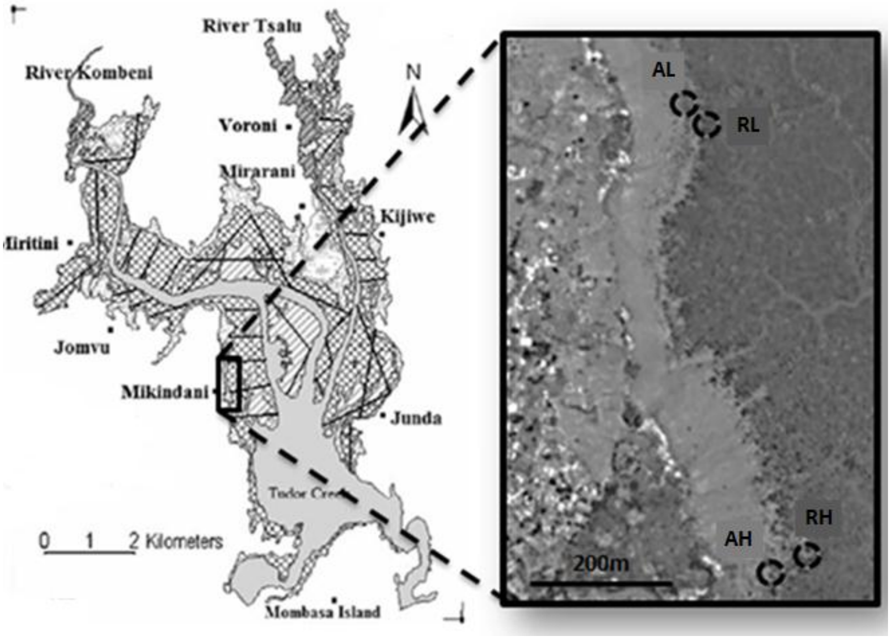


Figure 2.1: Location of study sites on the boarders of the mangrove forests of Mikindani, Mombasa (Kenya) which are reported to be silted (Mohamed *et al.*, 2009). Four study sites have been selected based on the species difference and the siltation degree. *Rhizophora mucronata* and low siltation (RL); *Rhizophora mucronata* and high siltation (RH); *Avicennia marina* and low siltation (AL); *Avicennia marina* and high siltation (AH). (adapted from (Mohamed *et al.*, 2009)).

Distinction of the study site in a low silted site and a highly silted site has be made by means of different indicators. Some aspects were compared: (1) As seen above, suspended solids originating from the flush flood would result in a higher sand percentage in the substrate. However, sand has a lower water holding capacity, resulting in dryer soils. This is visually and physically easily distinguishable. (2) Bearing in mind the traveling path of the flush flood and the knowledge that more suspended particles will sink closer near the source of the influx, the highest degree of siltation would be closest to the sea. (3) The steepness, population density and the landuse off the hill adjacent the mangroves would have a major effect on the degree of siltation (Fig 2.2). One may expect more siltation where the hillside is steeper and where landuse and human activity will provide less stabilization of the soil by the natural vegetation.

These assumptions were all met, making the choice of which site granted highly silted and which low silted justifiable. A soil sampling campaign was done to give a decisive answer of the correctness of this division, as will be discussed later on.

Figure 2.2: Hill slope adjacent the highly silted site, where agricultural practices loosen the soil, promoting erosion and runoff.

2.2 General site characteristics

2.2.1 Micro-climate

During physiological measurements the micro-climate was measured in the four different sites. The internal measuring devices of the porometer (AP4) (discussed in section 2.3.2.2) were used to measure temperature (°C), Photosynthetic active radiation (PAR) (µmol m^{-2} s^{-1}) and relative humidity (%) during sampling.

2.2.2 Soil characteristics

To estimate the natural variability of the soil, six soil cores (60 cm in depth) were randomly taken per site, three samples were taken during spring tide and the other three during neap tide, to comprise the highest natural variability of the soil within the study period. In the lab the soil cores were split in different soil layers (0-2; 2-4 ;4-6 ;6-9 ;9-15 ;15-20 cm) on which measurements of nutrients [µm], density [g m^{-3}], water content [%], porosity and grain size [µm] were performed. In the field, salinity [ppt], pH, dissolved oxygen [mg/L] (both measured using a YSI multiparameter meter), colour and width of these soil layers were measured or estimated.

In the lab, nutrients were extracted from weighted samples (~10 g wet weight) by adding 40 ml of 1N KCl. After shaking this solution for at least 1h, centrifugation was applied. According to the methods described by Parsons (1984) and APHA (1998), the nutrients in the obtained supernatant were analysed. Orthophosphate (PO_4^{3-}P) was determined using the ascorbic acid method at 885 nm, ammonia (NH_4^+-N) was determined using the indophenol method at 630 nm after at least six hours and dissolved nitrate and nitrite ((NO_3^- and NO_2^-)-N) was determined using cadmium reduction method and measured colorimetrically at 543 nm. Analytical quality check was carried out by running procedural blanks alongside the samples as well as through the use of check standards. All chemicals used for analysis were of analytical grade and all the glassware were pre-washed in acid before use.

2.2.3 Tree sampling

At the different sites, leaf and branch characteristics were measured. To select the trees of which the leaf and branch samples were taken, the tree selection procedure was standardized. Mature trees of approximately the same height and stem circumference were selected. Tree height was determined by using trigonometry as depicted in Fig 2.3. Stem diameters were measured with the help of a tape measure. For *Avicennia* trees, the diameter at a height of 130 cm (D_{130}) above ground level, also indicated as the diameter at breast height (DBH), was measured (Brokaw *et al.*, 2000). When the stem was forked below a height of 130 cm, every individual branch was treated as a separate stem. For

Rhizophora trees on the other hand, the stem diameter was measured 30 cm above the highest prop root, for the ease of this report we will indicate this measure as D_{30}.

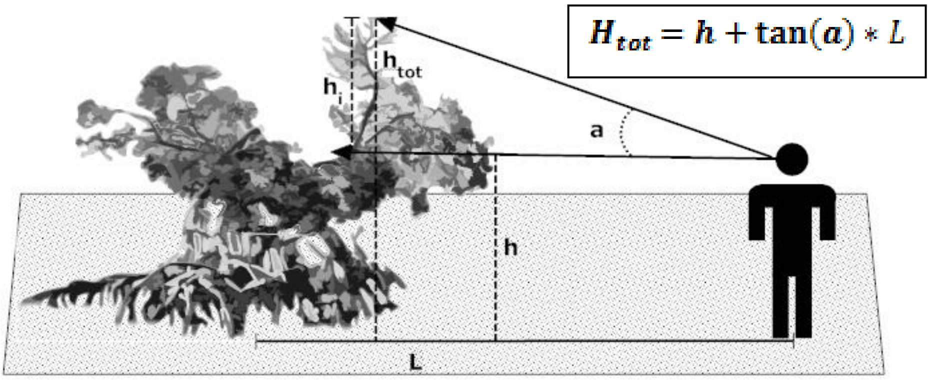


Figure 2.3: (A) Measuring the height of a mangrove tree using the rules of trigonometry. L: Distance between stem and point of measuring; h: researchers eye height; a: The angle formed by the horizontal line at eye height and the line between the researchers eye and top of the tree; h_i: Calculated height of the tree above the horizontal at eye height; h_{tot}: the total height of the tree.

For stomatal resistance experiments, 5 randomly but standardised trees were selected per plot, making a total of 20 trees, 10 *Rhizophora mucronata* and 10 *Avicennia marina* trees, equally subdivided over high and low siltation sites. During the 10 measuring days for hydraulic conductance, one standardised tree per plot was randomly selected each day, making a total amount of 10 selected trees per study site.

2.3Leaf characteristics

2.3.1 Leaf sampling

To standardise the leaf characteristics, one of the leaves of the third leaf pair (Fig 2.4) was selected as suitable for physiological measurements, based on the assumption that these leaves are active and mature. Other used standardizations include the choice of leaves at approximate the same height above ground level, which were fully sun exposed and oriented roughly at same the wind direction.

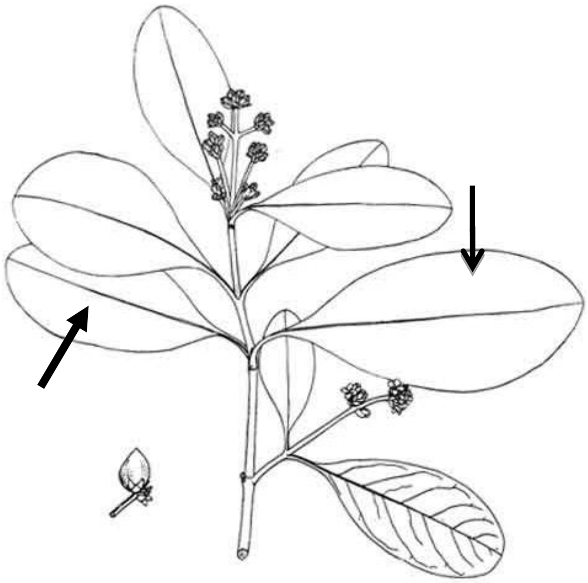


Figure 2.4: Arrows indicate the leaves of the third leaf pair.

For measurements of stomatal conductance and leaf anatomy, five leaves of five different trees were selected per site and marked as representatives for the whole site. The choice for picking five representative trees and only one leaf of each tree was a balance between feasibility and the need to cover the highest possible variability between trees within a particular area, not the variability within a tree. Representative trees and leaves were therefore chosen (With the help of experienced mangrove researchers Prof.dr.Nico Koedam, Judith Okello and George Onduso) bearing in mind the minimization of intra-tree variation.

2.3.2 Leaf water content, leaf number and leaf size

Per branch, the leaf area of 20 randomly picked mature leaves was measured using a Portable Laser Leaf Area Meter (CI-202L). Afterwards, this selection of 20 fresh leaves was weighed and put overnight in the oven (65°C) to acquire the dry mass weight. The difference between both weights resulted in the leaf water content.

In addition, all other leaves of the branch were counted and measured with the leaf scanner to obtain the total leaf number and total leaf area per branch. From these data the average leaf size was calculated.

2.3.3 Stomatal characteristics

A stomatal print of the *Rhizophora* leaves was accomplished using nail polish (Steppe, 2011). Due to the hairy habitus and the sunken stomata of the *Avicennia* leaves, it was not possible to use the same protocol as for the *Rhizophora* leaves. As an alternative, the technique of maceration was applied, with a comparable result. The epidermis layer was easily removed by placing the leaves bathing in a maceration solution during 10h in a 65°C oven. A maceration solution contains 5 parts hydrogen peroxide (H_2O_2) and 1 part of glacial acetic acid (CH_3COOH). Afterwards, the lower epidermis peel, containing the stomata, was stained using blue-safranin mix and fixed by glycerine.

Four separate positions per slide were chosen, as an attempt to comprise the variability, and were photographed by a microscopic camera (Colorview IIIv soft imaging system 0.63x1/2”=11.5; 2/3=17.5), making further analysis with the software Cell-D possible.

Not only the number of stomata was counted, but also the width and length of 15 randomly picked stomata were measured. These data was further used to calculate stomatal density [mm^{-1}], stomatal area [µm²] and total lumen area per total leaf area. The formula of the last 2 calculations is equivalent with equation 2.5 and 2.7, using stomata density instead of vessel density.

2.3.4 Stomatal resistance

The stomatal resistance was measured by the use of an automatic porometer (AP4), which due to technical restrictions was only calibrated once, just prior to the measurement campaign. Calibration was performed under a relative humidity of 40% and 27°C. The pincer was always placed on a predetermined permanent position in the middle, just aside the midrib, of a leaf, to avoid variation due differences in stomatal density within a single leaf. The AP4 was placed on the leaf until equilibrium was reached, but special attention was made placing the pincer no more than 2 minutes on the leaf , avoiding stomatal closure due to shading, caused by the device itself. In case this condition was not satisfied, corresponding data was removed from the dataset.

Stomatal conductance was measured on sunny days in trees of both silted and less silted areas. During one measuring day, only one species was handled to assure a high measuring frequency. The experiment started from sunrise (6:30 a.m.) until sunset (6:30 p.m.), which results in 8 cycles of data collection. Since 45 minutes were needed to measure all five selected leaves per study site, a complete measurement containing both sites, needed 1h30. Most of the cycling time was claimed by relocation of the observer between both sites.

The m/s units of the porometer data were converted to mmol m^{-1} s^{-1} by using the formula of Jones (1992):

$$y = \frac{43.917 - 0.1424 * T_a}{(x - 1000)} \tag{2.1}$$

With: T_a: *the air temperature [°C]*

X : *stomatal resistance [s* m^{-1}*]*

Y : *stomatal conductance [mmol* m^{-2} s^{-1}*]*

After the last measurement day, all selected leaves were sampled, and places into a mixture of 70% ethanol (CH_3CH_2OH) and some glycerol ($C_3H_5(OH)_3$) for later determination of the stomatal anatomy. The vapour pressure deficit of the air (Da) [KPa] was calculated for the measurement days, since it has an important influence on the stomatal conductance and the water flow in trees. Goldstein *et al.* (1998) defined the value of Da as the difference between saturation vapour pressure at air teperature (e^0_V) [KPa] and ambient vapour pressure (e_V) [KPa]. These variables were calculated as follows:

$$D_a = e_V^0 - e_V \tag{2.2}$$

$$e_v^0 = 0.6108 exp\left(\frac{17.27T_a}{T_a + 237.3}\right) \tag{2.3}$$

$$e_V = e_V^0 * \frac{RH}{100} \tag{2.4}$$

With: *Ta: the air temperature [°C]*

RH: the relative humidity of the air [%]

2.4Branch characteristics

For each site, branch anatomy and hydraulic conductivity are determined in the same samples. Hydraulic conductivity is an important feature as it influences sap flow which is of vital importance for the internal water regulation in a tree and is therefore an important indicator of stress within a tree caused by siltation. Relating hydraulic conductance of randomly picked branches, representing the mangrove trees, to the different degrees of siltation will give information about the potentially negative effect of siltation on the mangrove trees.

2.4.1 Branch sampling

Each day, out of 10 measuring days, one representative tree for each site (AH, AL, RH, RL), was randomly chosen, resulting in a total of 20 branches per study site sampled on 10 different trees. Only trees of approximate the same height which were not damaged by cuttings were selected to avoid potential effects on the measurements due to these cuttings.

Within the selected trees, two branches were marked that satisfied the requirement of having a diameter of 10 mm, a low number of knots, fully exposed leaves and an approximately equal height above ground level. One of these branches was sampled in the morning, while the other one was sampled in the afternoon. Sampled branches of *Avicennia* trees were on average 130 cm in length, while those for *Rhizophora* were on average 60 cm long.

Sampling was done using a specific procedure whereby a placemat is wrapped around the branch, forming a funnel. Before removing the branch, the funnel is filled with water, so the cutting took place under water avoiding potential cavitation (Hao *et al.*, 2009). After cutting, the branch is immediately placed in a dark coloured bag containing a humid sponge. The high humidity created by the sponge prevents further water loss by evaporation of the branch and by transpiration of the leaves.

In the lab, the sampled branches were further subdivided into three parts (Fig 2.5). These re-cuttings were again performed under water, as a precaution for vessel embolism. The lowest 10 cm (part A, Fig 2.5) of the branch was not used due to potential embolism during transport. The subsequent 15 cm long part of the branch (part B, Fig 25) was used in the experimental set-up of the hydraulic conductivity. After measuring the hydraulic conductivity, a 5 cm piece of branch was cut off, labelled and placed into a mixture of 70% ethanol (CH_3CH_2OH) and some glycerol ($C_3H_5(OH)_3$). This mixture was used for preservation of the branch part for anatomical research. The remaining part of the branch (part C, Fig 2.5) containing the leaves, was used later to determine some of the leaf characteristics as described in section 2.3.2.

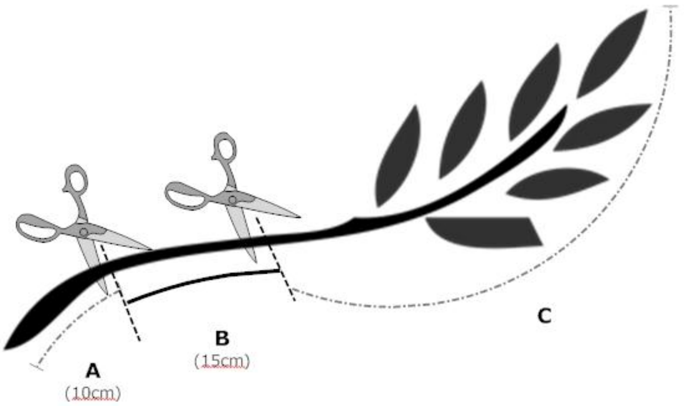


Figure 2.5: Subdivision of sampled branches in part A (the first 10cm), part B (the subsequent 15cm) used in the experimental set-up, and part C (the remaining part of the branch) used in later leaf experiments.

2.4.2 Branch anatomy

Five of the preserved 5 cm long branch parts per site, were used for making anatomical transverse wood slides of 25 µm thick with a Core-Microtome (Gartner *et al.*, 2010). These wood slides were subsequently coloured using a safranin ($C_{20}H_{19}N_4^+$, Cl^-) and alcian blue ($C_{56}H_{68}Cl_4CuN_{16}S_4$) mixture before three different lateral positions per slide were photographed by a microscopic camera (Colorview IIIv soft imaging system 0.63x1/2”=11.5; 2/3=17.5). Further analysis were performed with the software Cell-D. For more details on this protocol can be found in (Jansen *et al.*, 1998; Rapp *et al.*, 1998; Ruzin, 1999).

The width (a) and length (b) of 20 randomly selected vessels were measured (Fig 2.6a). From these measurements, vessel area [µm²], vessel density [mm^{-1}], equivalent vessel diameter (D_e) [µm²], conductive area per wood area [-] and phloem ratio [%] were calculated as follows:

Vessel Area: $$\pi * \frac{a}{2} * \frac{b}{2} = A_{vessel} \qquad (2.\ 5)$$

D_e: $$\sqrt{\frac{2a^2b^2}{a^2+b^2}} = D_e \qquad (2.6)$$

Conductive area: $$\frac{A_{vessel} * VesselDensity}{A_{Cross\ section}} = A_{conductive} \qquad (2.7)$$

Phloem ratio: $$\frac{Area\ 1}{Area\ 2} \qquad (2.8)$$

With: *Area 1: phloem tissue (Fig 2.6b)*
Area 2: xylem tissue (Fig .2.6b)

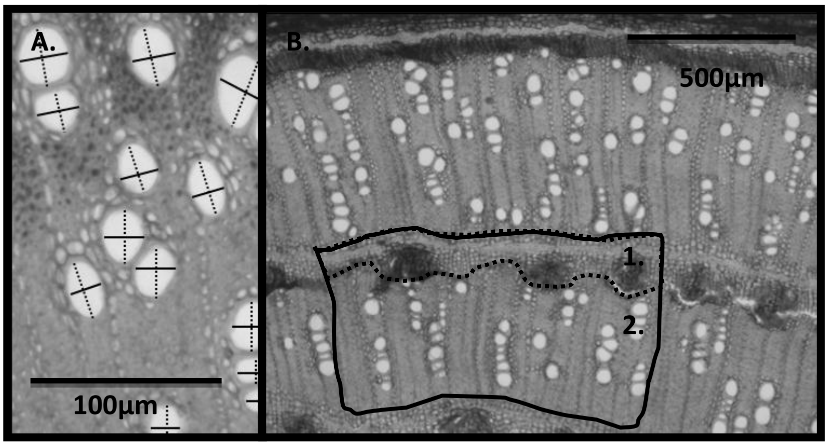


Figure 2.6: Photographs of anatomical transverse slides of selected branches. A: Measuring vessel length (dotted) and width (full); B: *Avicennia marina*; 1. indicating the girdle of phloem (the dotted frame), divided by the total growth layer , indicated with number 2 (the full frame) resulting in the phloem ratio.

2.4.3 Hydraulic conductivity

The hydraulic conductivity (Angeles *et al.*, 2002; Lopez-Portillo *et al.*, 2005) is based on the individual sap flow. A clarifying scheme of the set-up is given in Figure 2.7. After weighing part B of the branch, it is subsequently placed within the set-up (Fig 2.7B) oriented so that the end, which is normally closest to the stem of the tree, is pointing toward the influx of the solution flowing through the set up. The syringe (Fig 2.7A) and all tubes, contain a 1% concentration of filtered seawater which is similar to the ionic concentration of the sap within a mangrove tree (Scholand *et al.*, 1966; Ball, 1988b; Stuart *et al.*, 2007; Choat *et al.*, 2011). Adjusting the height of the syringe will result in an alteration of the pressure force of the solution on the one end of the branch. On the other side of the branch, a pipet (0.1 mm) filled with loading dye (Fig 2.7C) is placed upon graph paper (Fig 2.7D). At a certain height of the syringe, the pressure created will push the diluted seawater through the branch. The sap coming out of the other end of the branch will on its turn push away the loading dye. This movement is photographed every 30 seconds during 5 minutes (Canon, Eos D1000). Using the software ImageJ, the speed of the loading dye could be determined. Knowing the pressure generated by the height of the syringe, the volume of the pipet and the speed of the loading dye, sap flow through the branch can easily been calculated. Applied pressure [Pa] on the branch is calculated as shown in equation 2.9, using density of the fluid, acceleration due to gravity and the height of the syringe. Specific and hydraulic conductivity was calculated using respectively equation 2.10 and 2.11:

$$\Psi = h \times \rho \times g \tag{2.9}$$

With: h: applied height [m]

Ψ:applied pressure [Pa]

ρ: density of the fluid [kg m^{-3}]
g: acceleration due to gravity [m ^{1}s^{-2}]

$$K_h = \frac{F \times \rho}{\Psi} \tag{2.10}$$

$$K_s = \frac{K_h}{A} \tag{2.11}$$

With: *F: Sapflow rate [m^{-3} s]*
K_s: Specific conductivity [mmol m^{-1} s^{-1} MPa^{-1}]
K_h: Hydraulic conductance [mmol m s^{-1} MPa^{-1}]
A: Wood area [m²]

Before and after this experiment, all examined branches were weighed, bearing in mind that the difference between both measurements gives an indication of water uptake or loss by the branch during the experiment.

After weighting, a 5 cm long part of the examined branch was cut, placed vertically on the graph paper and was photographed for measuring bark, wood (used in equation 2.11) and pith area using ImageJ. Afterwards, this piece of branch was labelled and placed into a mixture of 70% ethanol (CH_3CH_2OH) and some glycerol ($C_3H_5(OH)_3$). This mixture was used for preservation of the branch part for anatomical research.

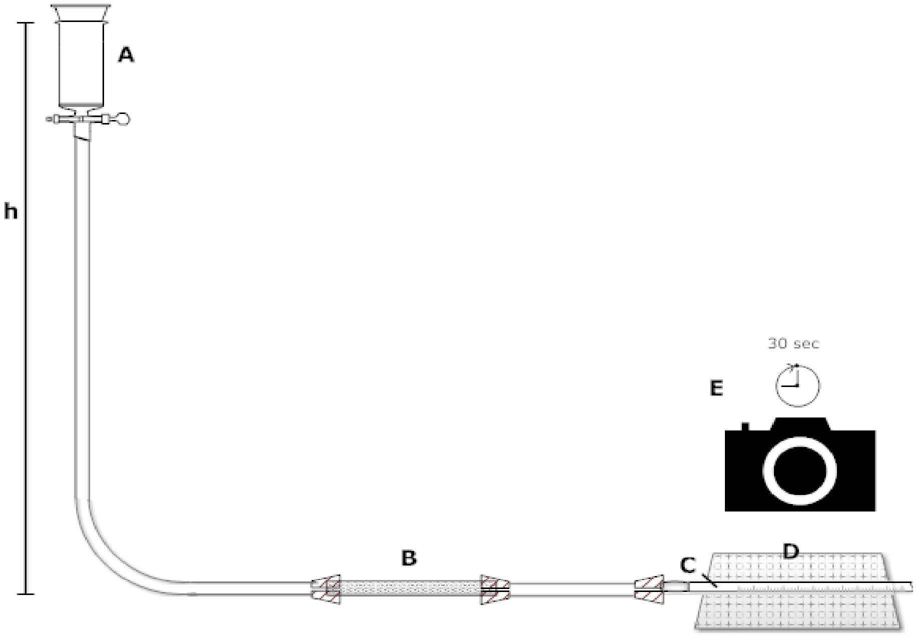


Figure 2.7: Experimental set-up for sap flow measurements. h: height of syringe; A: syringe; B: branch; C: pipet (0.1 mm) containing loading dye; D: graph paper; E: camera.

2.5Root characteristics

Many researchers (Robertson *et al.*, 1989; Steinke *et al.*, 1993; Frusher *et al.*, 1994; Lee, 1998; Lee, 1999; Cannicci *et al.*, 2008) have indicated the importance of crabs within a mangrove ecosystem, in particular there interaction with the performance and carbon cycle of the mangrove trees. The burrows provide an efficient pathway to flush the salt which has accumulated on the roots, resulting in more favourable conditions for the trees (Stieglitz *et al.*, 2000). Aside from this, these burrows will increase the soil aeration (Smith *et al.*, 2009). Therefore, in this research we performed a side observation, counting crab burrows in the direct environment of each tree corresponding to the method explained by Skov (2002). A square of two meters by two meters was randomly placed around a tree, followed by the random placement of three smaller squares, with a length and width of 50 cm, in which crab holes were accurately counted (Fig 2.8). These holes were subdivided into 2 size classes depending on the diameter of the entrance of the crab holes (<1 cm and ≥1 cm). Since a mutually beneficial association between crabs and roots of *Avicennia marina* may exist (Kristensen *et al.*, 2006) and there contribution to oxygen in the rhizosphere (Kitaya *et al.*, 2002), the number and respective height of the pen roots in the direct environment near *Avicennia* trees were measured and subdivided into height classes per 5cm.

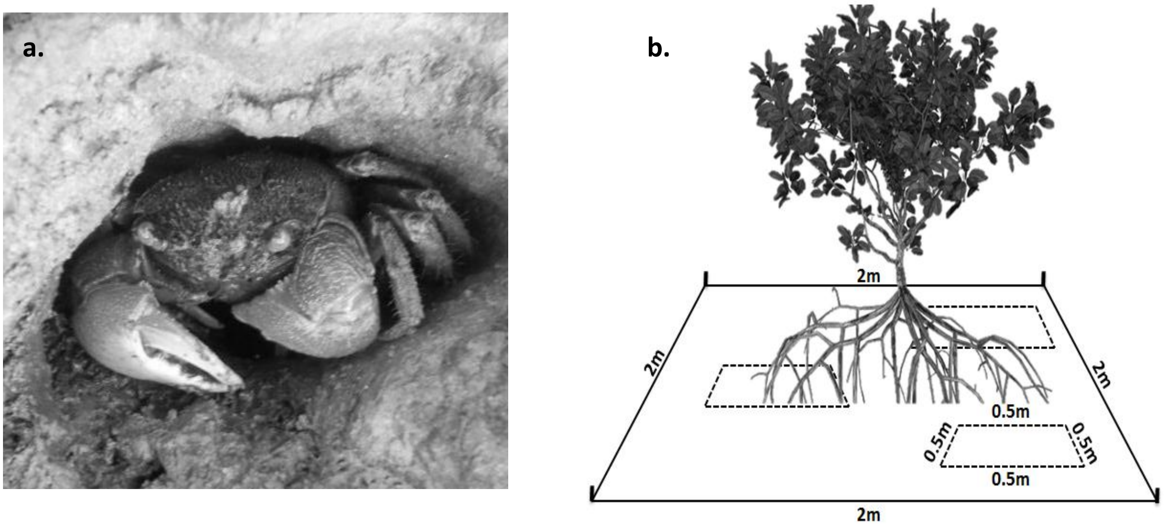


Figure 2.8. (a) Mangrove crab hiding between roots of *Rhizophora mucronata* tree; (b) Method for counting crab burrows according to Skov (2002) using a square of two by two meters randomly placed around a tree and by the random placement of three smaller squares, with a length and width of 50 cm.

2.6 Statistical data analysis

The software Statistica (version 8.0 StatSoft Inc., Tulsa, USA) was used for all statistical analyses of the data. Since the assumptions for parametric testing were not met, the non-parametric Mann Whitney U test was used to compare silted with less silted study sites.

CHAPTER 3

3 Results

3.1 General site characteristics

The micro climate of all trees was characterised by measuring abiotic characters like relative humidity [%] and temperature [°C] in the morning and in the afternoon. Biotic tree characteristics measured were cross sectional area at D_{130} [cm^2], three height [m], height where the branch was cut [cm] and the number of branches per tree [-]. All these characteristics of the four sites (Table 3.1) did not significantly differ ($p>0.05$). However for *Rhizophora* trees, a slight difference in the branching pattern (number of branches) could be a subject of discussion, although no statistically significant difference was found.

Table 3.1. Biotic and abiotic characteristics of the study site and the sampled *Avicennia marina* (A) and *Rhizophora mucronata* (R) trees located within the high siltation (H) and low siltation (L) sites. The number of decimals is assigned conform the precision of the measuring equipment. n is the number of measurements per study site.

		Low siltation		High siltation		n
		A	R	A	R	
micro-climate	RH (a.m.) [%]	68 ± 4	67 ± 3	67 ± 3	66 ± 4	10
	RH (p.m.) [%]	61 ± 4	62 ± 5	61 ± 4	62 ± 3	10
	T (a.m.) [°C]	28.6 ± 1.5	29.3 ± 1.3	28.9 ± 1.0	28.7 ± 1.3	10
	T (p.m.) [°C]	31.0 ± 1.4	30.7 ± 1.6	30.6 ± 1.6	31.0 ± 1.4	10
Tree characteristics	Cross sectional area at D_{30}/D_{130} [cm^2]	11.20± 7.87	11.68 ± 12.93	10.59 ± 3.52	8.27 ± 5.08	18-20
	Tree height [m]	3.06 ± 1.28	2.13 ± 0.26	2.85 ± 1.19	2.31 ± 0.17	20
	Height where branch was cut for sap flow experiments [cm]	132 ± 33	122 ± 20	131 ± 28	113 ± 16	19-20
	# branches	36 ± 10	20 ± 5	36 ± 12	27 ± 3	19-20
Soil analysis	Sand fraction [%]	53.2	61.3	65.9	63.9	
	# distinct soil layers	3	3	4	4	
	Dissolved oxygen in upper 10 cm [mg L^{-1}]	3.1	3.2	5.7	5.4	
	Salinity [ppt]	55.0	49.5	53.0	48.0	
	Redox potential	-43.0	-65.8	-14.5	-55.0	

Soil analysis (Table 3.1) indicated a higher sand fraction [%] and a higher number of layers for the high siltation sites. But also the amount of dissolved oxygen [mg L^{-1}] and the redox potential in the upper 10 cm soil layer were higher within the high siltation site. The salinity however was found higher in the low siltation site. Another interesting result is that for the top layer (upper 10 cm) the nutrients (Phosphates, nitrates and ammonia) were higher in the low silted sites, however, at a depth around 10 cm the tables were turned, with higher nutrient for the high siltation site.

3.2Leaf characteristics

3.2.1 Leaf water content, leaf number and leaf size

Table 3.2 and Figure 3.1 visualise the results of the experiments comparing leaf characteristics, such as single leaf area [cm²] (Fig 3.1a,d), total branch leaf area [cm²] (Fig 3.1, b, e) and number of leaves per branch [-] (Fig 3.1c,f) of *Avicennia* (a-c) and *Rhizophora* (d-f) trees from high siltation and low siltation sites. The leaf characteristics of *Rhizophora* ($p<0.05$) point out that the trees in high siltation have a significantly smaller single leaf area as compared to trees in low siltation sites (Fig 3.1d). No other significant differences ($p>0.05$) were observed. The branches of trees on silted substrate have more leaves per branch but these are smaller for both tree species.

Table 3.2. p-levels for *Avicennia marina* and *Rhizophora mucronata* resulting from Mann-Whitney U test (confidence interval of 95%) performed for different leaf characteristics. Statistical relevant differences (p <0.05) are indicated by an asterisk (*)

		p-level	
		Avicennia	***Rhizophora***
Single leaf area [cm²]		0.0808	0.0131*
Total branch leaf area [cm²]		0.5503	0.7132
# leaves / branch [#]		0.0695	0.0565
Fresh leaf mass per area [g/cm²]	**a.m.**	0.6911	0.0015*
	p.m.	0.1415	0.0008*

The fresh leaf mass per area, which is the result of dividing the mass of fresh leaves [g] by their respective total leaves sizes [cm²], approximates the amount of water in the leaves. For this particular experiment, a distinction is made between species, high siltation or low siltation sites and the time of sampling (a.m. or p.m.) (Fig 3.2).

Avicennia (Figure 3.2, a) has on average a significantly ($p<0.05$) lower fresh leaf mass per area compared to *Rhizophora*, indicating that the leaves of a *Rhizophora* tree hold more water than the leaves of *Avicennia* trees. The fresh leaf mass of al sampled leaves of *Avicennia* are very similar, except the *Avicennia* leaves sampled in the afternoon in low siltation sites ($p<0.1$) which are higher. This suggest that the *Avicennia* leaves of trees in a low siltation site gain more water in the afternoon.

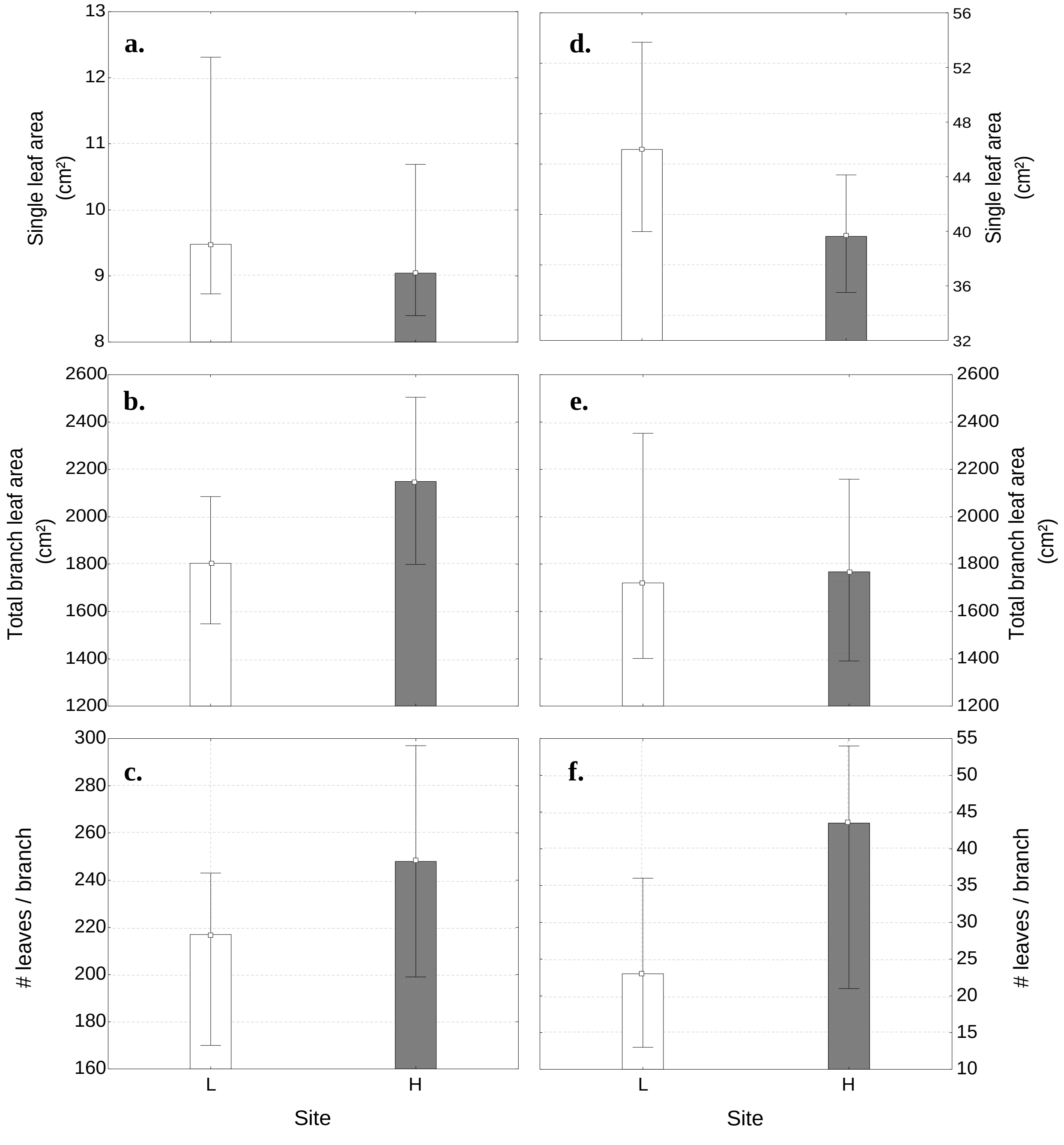


Figure 3.1. Leaf characteristics of *Avicennia marina* (a-c) and *Rhizophora mucronata* (d-f) growing in high siltation (H) and low siltation (L) areas. Data plotted are medians with 25 % and 75%, n = 14.

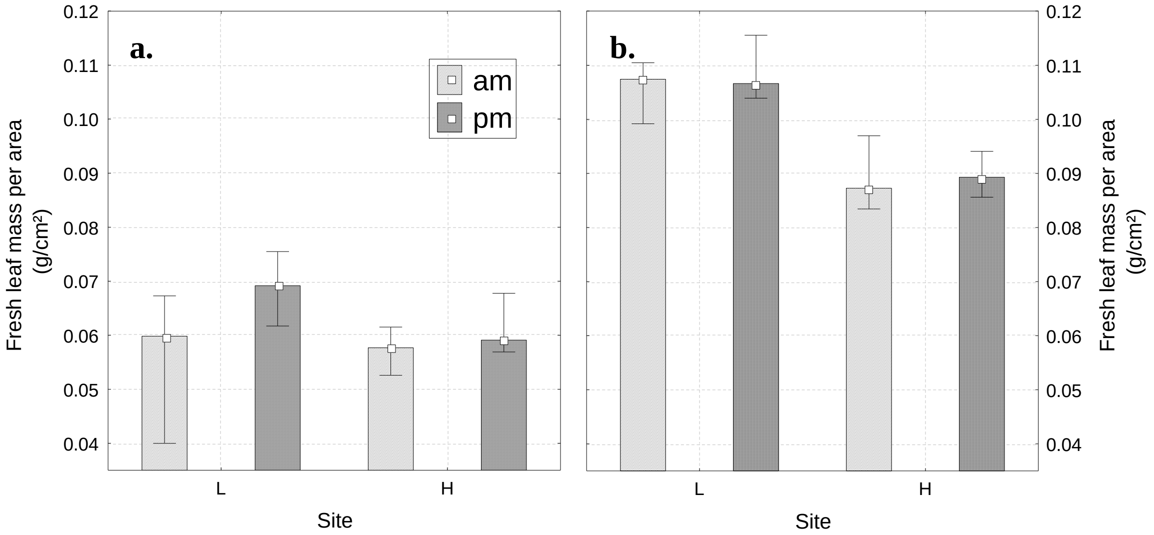


Figure 3.2. Mass of fresh leaves [g] divided by their respective total leaf area [cm²] for *Avicennia marina* (a) and *Rhizophora mucronata* (b) trees growing in low siltation (L) and in high siltation (H) sites. Difference in time of sampling is shown by single and double shaded bars, respectively for sampling in the morning (a.m.) and in the afternoon (p.m.). Plotted data are medians, 25% - 75%, n = 7-9.

For *Rhizophora*, the fresh leaf mass per area within the high siltation sites is significantly ($p<0.05$) lower compared to the low siltation site (Fig 3.2, Table 3.2). The difference in water content of the leaves compared between sites is independent of the time of sampling. On the other hand, the per site condition, by which is meant high siltation or low siltation condition, no difference can be noticed in fresh leaf mass per area between time of sampling.

Figure 3.3 shows the correlation between the average vessel area (μm^2) and the total leaf area of a branch (cm^2). Remarkably, the r^2-value for data gathered from silted sites is very high, suggesting a strong correlation between both variables. The r^2 value for *Avicennia* and *Rhizophora*, both in silted environment, are respectively 0.870 and 0.971. This high correlations was absent for the less silted trees, as shown by an r^2-value near zero for *Avicennia* as well as *Rhizophora*.

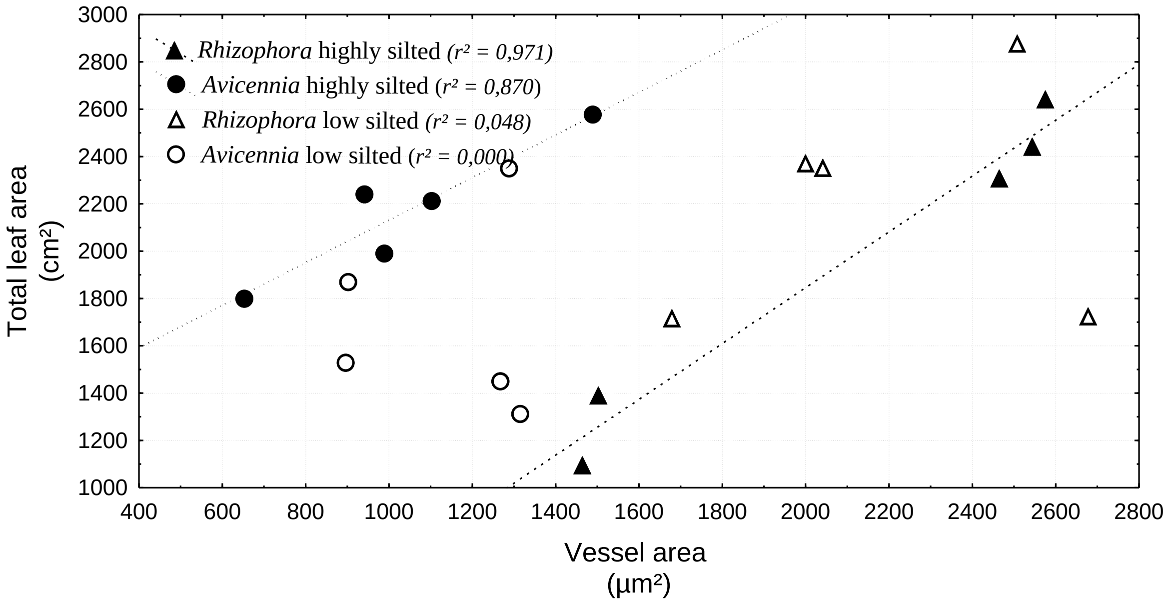


Figure 3.3. Total leaf area in function of vessel area for *Avicennia marina* (circles) and *Rhizophora mucronata* (triangles) branches, sampled in less silted (white) or silted (black) areas. Linear regressions are fitted for the data of both mangrove species positioned in the silted sites. n = 5.

3.2.2 Stomatal characteristics

All stomatal leaf characteristics of *Avicennia* were statistical significantly different ($p < 0.05$) between samples originating from high siltation and low siltation sites, whereas for *Rhizophora*, only the stomatal area significantly differ. A significantly ($p<0.05$) higher stomatal density was found on the leaves of *Avicennia* trees in high siltation sites (figure 3.4a). In contrast, the stomatal area is significantly ($p<0.05$) higher for both *Avicennia* and *Rhizophora* trees, when they are sampled in low siltation sites. Hence, in the high siltation sites there are more, but smaller stomatal pores in the leaves.

Figure 3.4 c, f shows the pore area index, which is calculated by using stomatal density and stomatal area, for both species and both silted and less silted sites. The pore area index of *Avicennia* trees sampled in silted sites is significantly higher than for sampling in less silted sites. *Rhizophora* trees, however, a significant difference in pore area index was not found, when samples of high siltation and low siltation sites were compared.

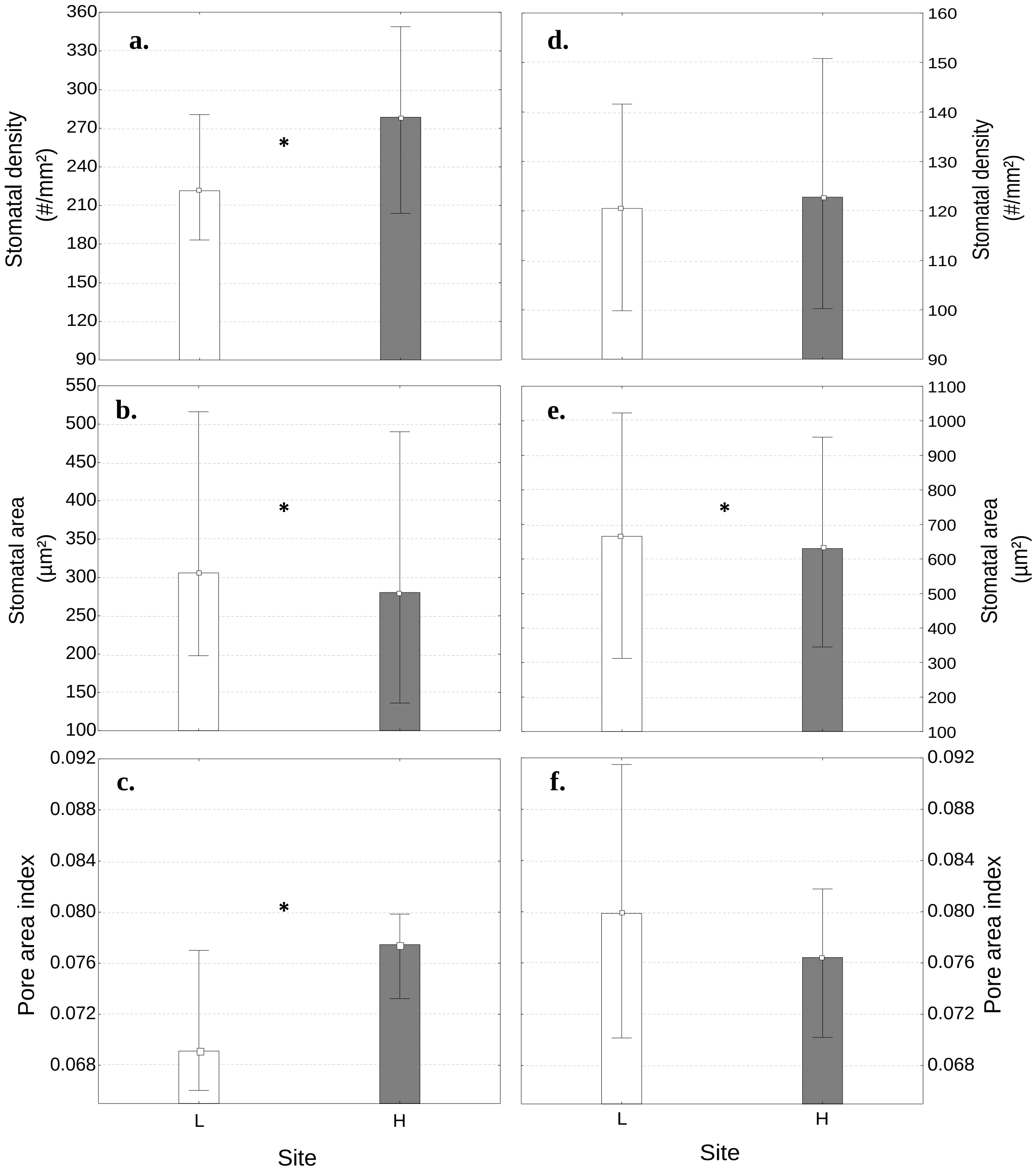


Figure 3.4. Stomal density (a,d), stomatal area (b,e) and pore area index (c,f) for *Avicennia marina* (a-c) and *Rhizophora mucronata* (d-f). Significant differences ($p<0.05$) between the low siltation (L) and the high siltation (H) sites are indicated by an asterisk. Data plotted are medians, minimum and maximum values of the dataset, $n_{(\text{stomatal area})} = 300$ and $n_{(\text{number of stomata and pore area index})} = 20$.

3.2.3 Stomatal resistance

To avoid misrepresentation of the results of the stomatal conductance experiment, the temperature [°C], the light [µmol m^{-2} s^{-1}] and the relative humidity [%] for both the silted and the less silted sites, per time category, were measured (Fig 3.5).

An overview of the measured stomatal conductance of the leaves of respectively *Avicennia marina* and *Rhizophora mucronata* of both silted and less silted sites are given in Figure 3.6 and Figure 3.7. As can be seen, the stomatal conductance of the less silted sites is in general higher than these for the silted sites per time category. Although this difference was not significant ($p>0.05$) for all time categories, it was for certain days as indicated by an asterisk in Fig 3.6 and Fig 3.7.

An interesting phenomenon is the correlation pattern between the vapour pressure deficit of the air and the stomatal conductance. For *Rhizophora*, no correlation was found for both sides (r^2-value was very low) (Fig 3.8). However, for *Avicennia*, the data formed a clear pattern resulting in a high r^2-value (Fig 3.9). As long as the vapour pressure deficit stays below 1.4 kPa, the stomatal conductance will decrease conform an negative exponential curve. Once the vapour pressure deficit rises above 1.4 kPa, no mayor fluctuations will occur, and the stomatal conductance will stay low. This pattern deviated a little for trees in high and low siltation sites: in the silted sites higher stomatal conductances are reached with low D_a-values, whereas lower stomatal conductance are reached at high D_a-values.

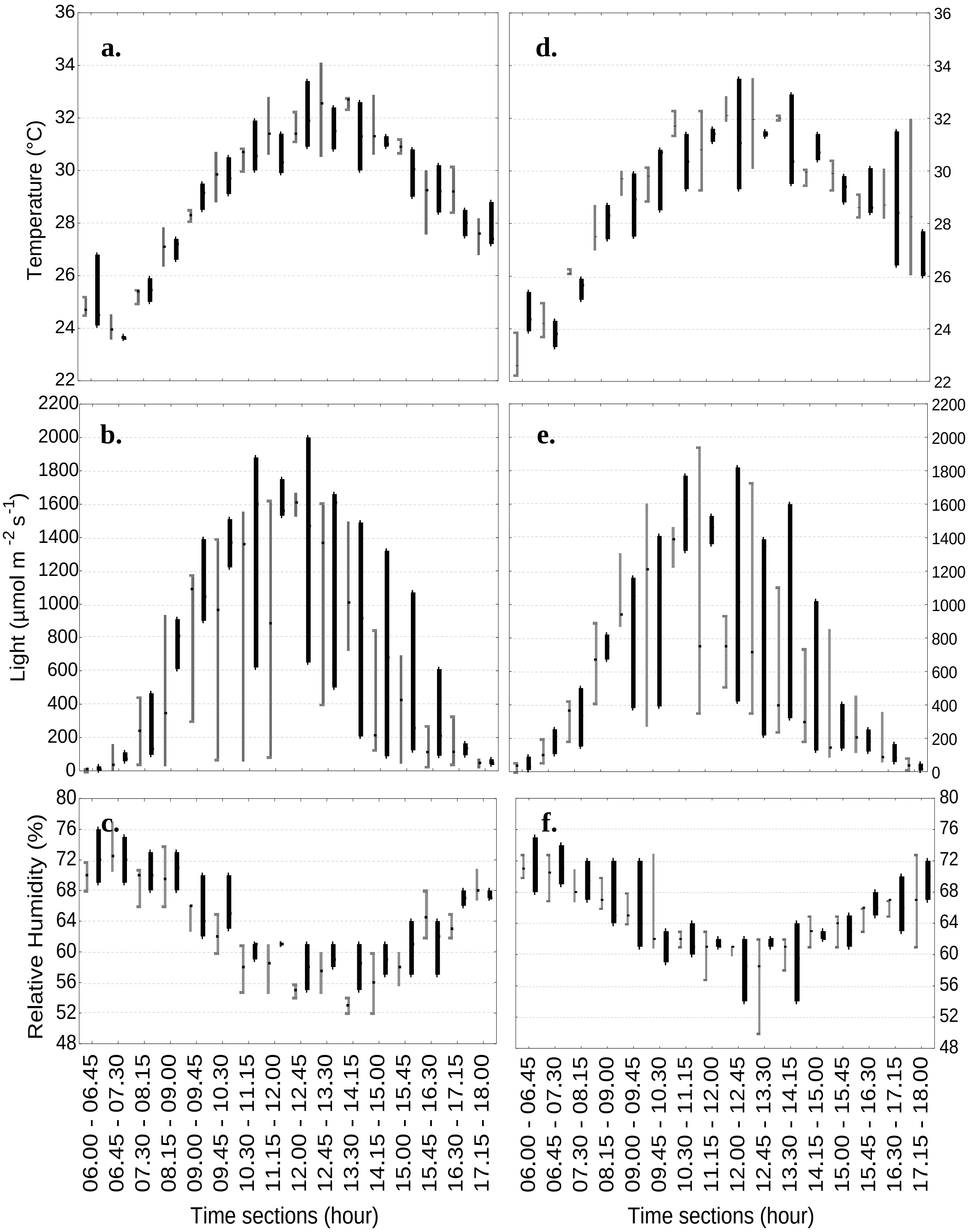


Figure 3.5. Temperature [°C] (a,d), light [µmol m^{-2} s^{-1}] (b,e) and relative humidity [%] (c,f) in plots of the mangrove species *Avicennia marina* (a-c) and *Rhizophora mucronata* (e- f), under different siltation levels. Data are represented in time sections of 45 minutes and grey and black whiskers represent measurements in low siltation and high siltation plots, respectively. Plotted values are medians, minima and maxima of the data sampled during the stomatal conductance measurements, n = 5-10.

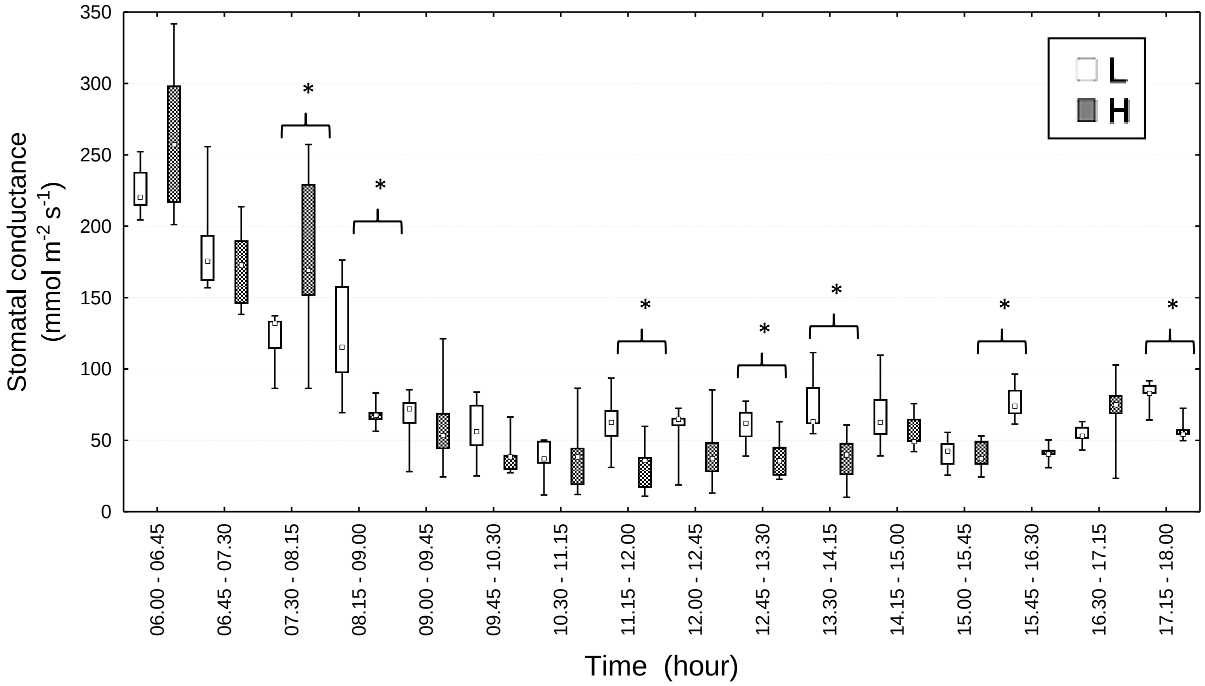


Figure 3.6. Stomatal conductance of *Avicennia marina* leaves. (L): Low siltation sites. (H): High siltation sites. Statistically significant differences ($p<0.05$) are indicated by an asterisk. Plotted data are medians, 25%-75% and the minimum and maximum values, n = 5-10.

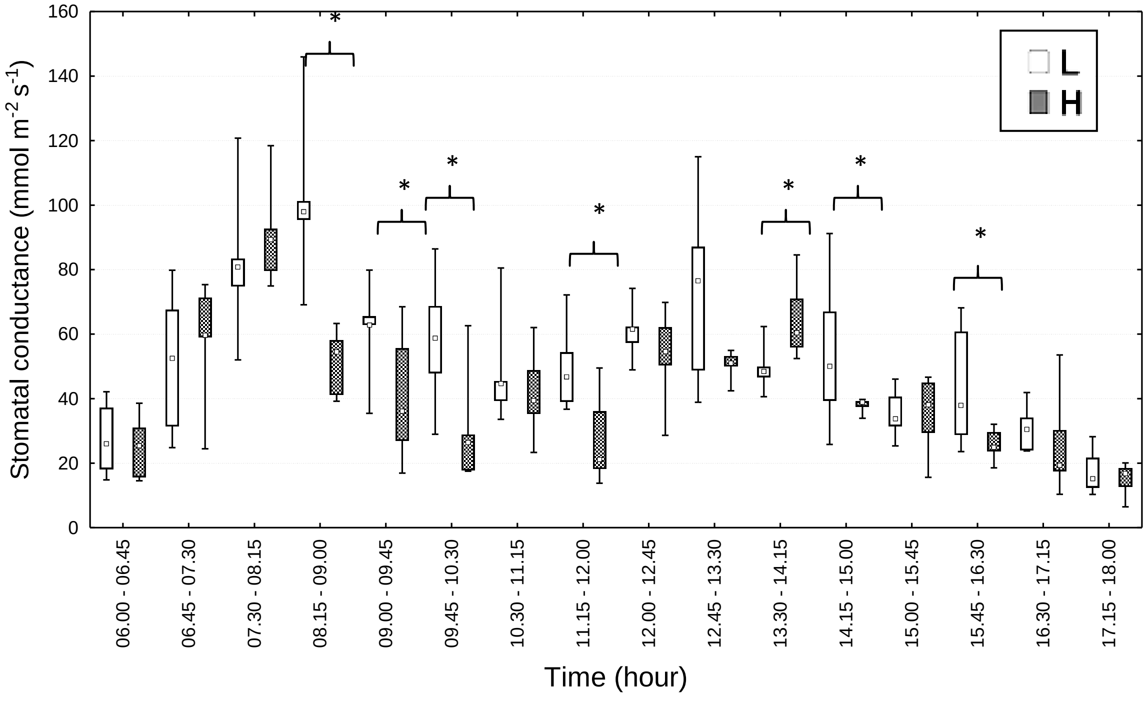


Figure 3.7. Stomatal conductance of the leaves of *Rhizophora mucronata* trees. (L): Low sited sites. (H): High siltation sites. Statistically significant differences ($p<0.05$) are indicated by an asterisk. Plotted data are medians, 25%-75% percentile and the minimum and maximum values are shown by error bars, n = 5-10.

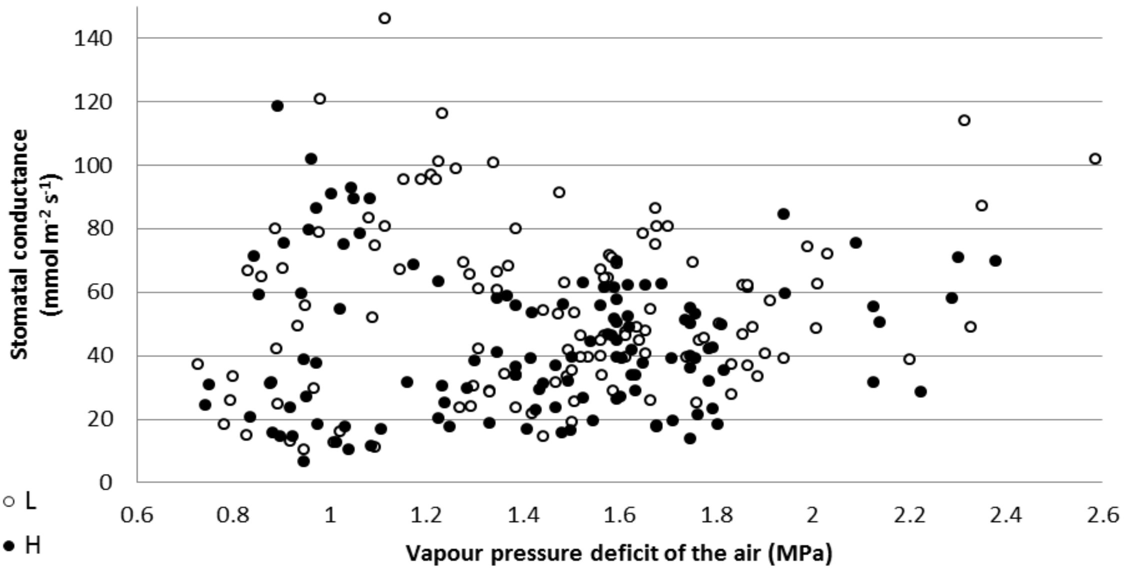


Figure 3.8 Relation between the vapour pressure deficit of the air and the stomatal conductance of the leaves of *Rhizophora marina* trees under high siltation (H) and low siltation (L)conditions, n = 120.

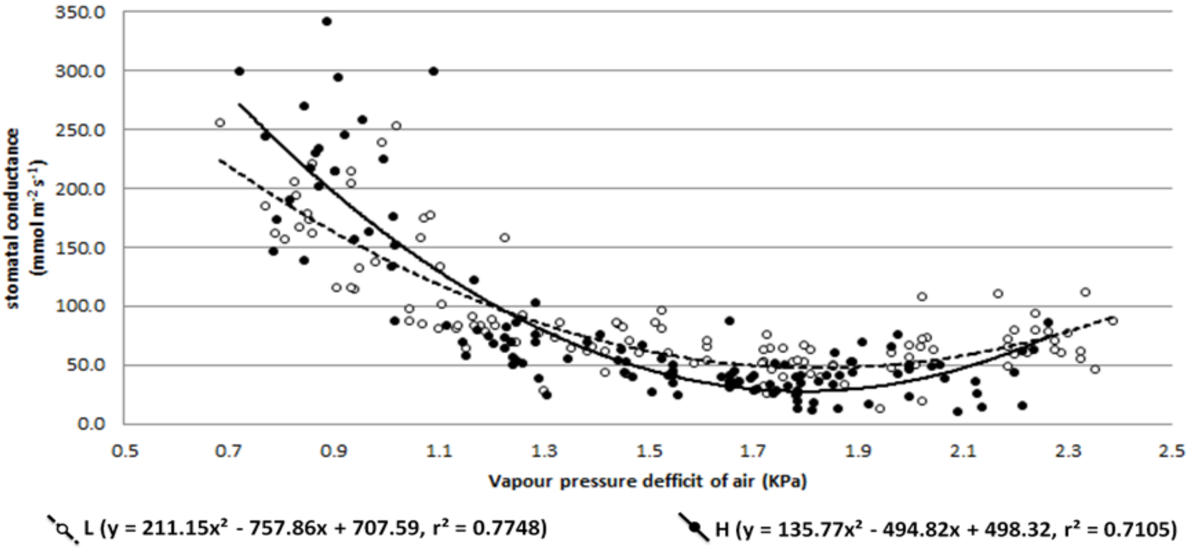


Figure 3.9 Relation between the vapour pressure deficit of the air and the stomatal conductance of the leaves of *Avicennia marina* trees under silted and less silted conditions. Lines indicates the best fitting polyline for the low siltation (L) and the high siltation (H) site, n = 120.

3.3 Branch characteristics

3.3.1 Branch anatomy

No statistically significant differences ($p>0.05$) in percentages of bark, xylem or pith area, measured on branch cross-section, are present for trees of the same species, despite the different degree in siltation (Fig 3.10). However, when comparing both species, strong differences can be noticed in there tissue distribution of their cross-sections. On average, half of the total cross sectional area of a *Rhizophora mucronata* branch is bark. The majority of the remaining area, which is on average 35% of the total cross-section area, can be assigned to xylem, leaving 15% of the total cross sectional area for pith area. *Avicennia marina* on the other hand has another subdivision of its cross-section. 80% of the total area is occupied by xylem, whilst the bark tissue area only covers 15% of the cross section area. No more than 5% of the cross-section area of an *Avicennia* branch is taken by pith area.

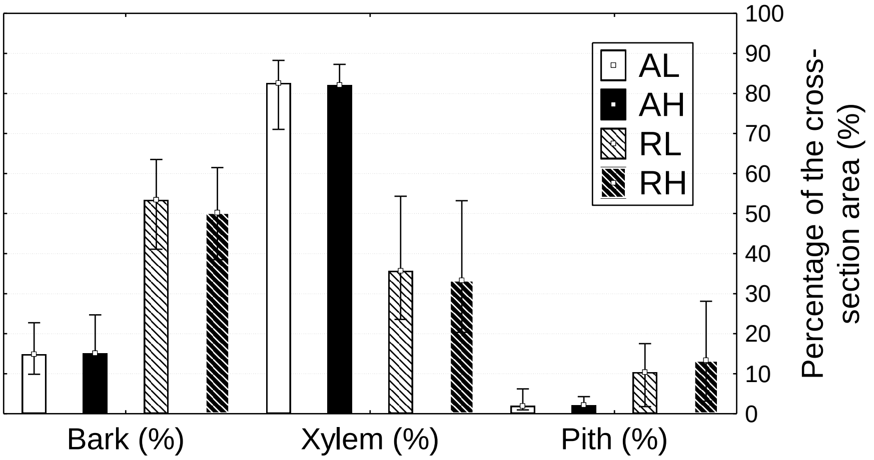


Figure 3.10. Tissue distribution measured on cross-sections of *Avicennia marina* (A) and *Rhizophora mucronata* (R) branches from high siltation (H) and low siltation (L) areas. Plotted data are medians with minimum and maximum values, n = 20.

No statistical relevant differences ($p>0.05$) were found for phloem ratio [%], vessel density [# vessels/mm² wood], vessel area [µm²] and the total conductive area (mm² vessel/mm² wood) of the cross sections for *Avicennia* trees, between high siltation and low siltation sites (Fig 3.11). Based on these results, one can conclude that the presence of a high siltation or low siltation underground beneath an *Avicennia marina* tree, does not result in a difference in vessel density (Fig 3.11b) or conductance (Fig 3.11d). However small non-significant ($p>0.05$) differences were noticed for both the phloem ratio per cross-section area and the vessel area: (1) A higher percentage of phloem ratio is noticed in the *Avicennia* branches positioned in a high siltation site (Fig 3.11a) and (2) *Avicennia* trees in low siltation area have the tendency to form vessels with a higher area (Fig 3.11c).

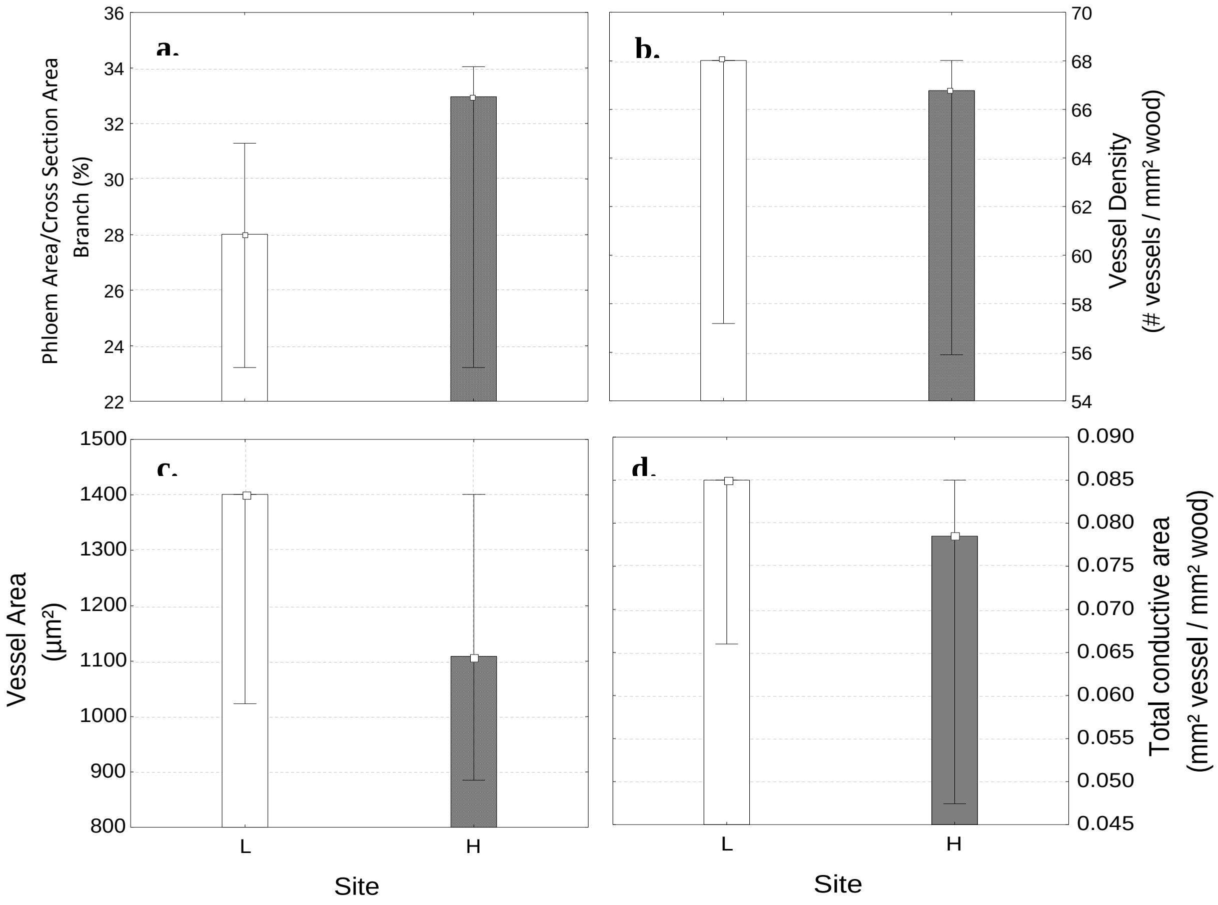


Figure 3.11. Anatomical characteristics, such as phloem ratio (a), vessel density (b), vessel area (c) and the total conductive area (d), of *Avicennia marina* branches of trees growing in high siltation (S) and low siltation (L) areas. Plotted data are medians with 25% -75%, n = 15.

Similar to *Avicennia* trees, the anatomical characteristics of *Rhizophora mucronata* are not significantly different (p>0.05) between high and low siltation conditions (Fig 3.12). Small non-significant (p>0.05) but noticeable differences were found for the vessel density (Fig 3.12a) and vessel conductivity (Fig 3.12c). No markedly differences in vessel area between both sites was found (Fig 3.12b).

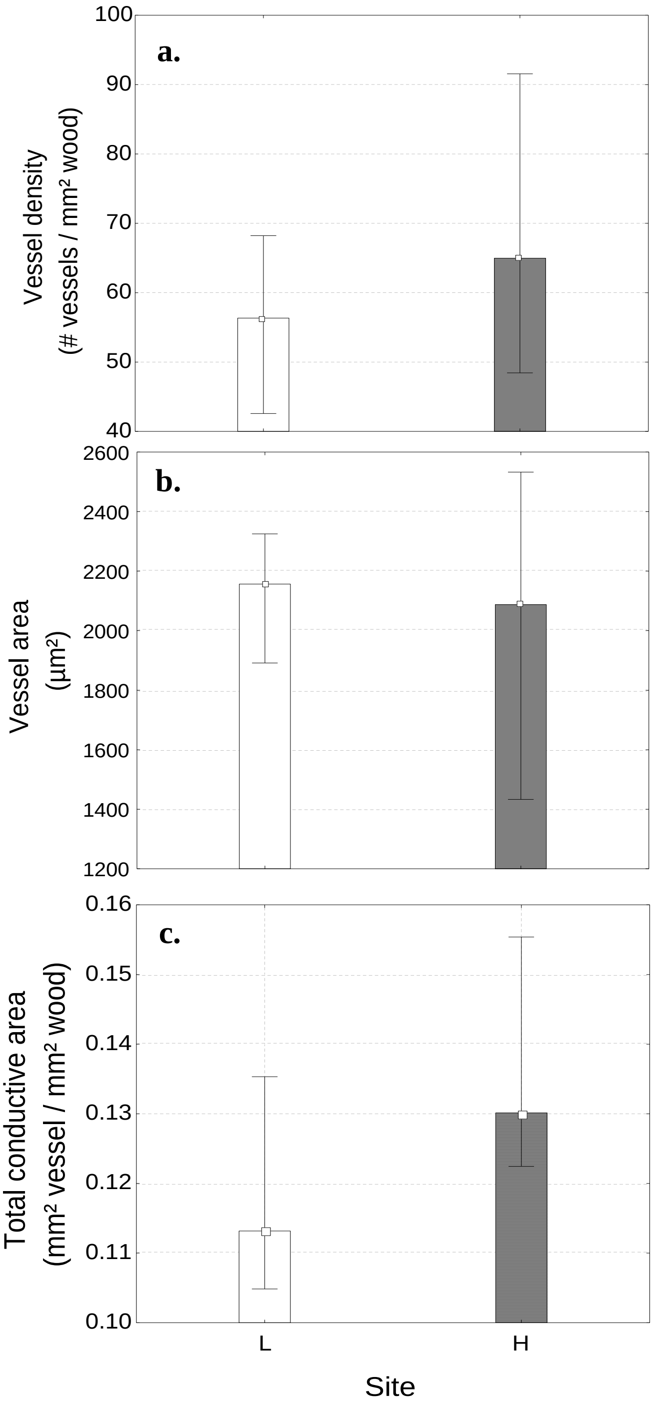


Figure 3.12. Anatomical characteristics - vessel density (a), vessel area (b) and the total conductive area (c), of *Rhizophora mucronata* branches of trees growing in high siltation (H) and low siltation (L) areas. Plotted data are medians with 25% - 75%. n = 15

3.3.2 Hydraulic conductivity

No noticeable or statistical differences in specific stem conductance [mmol m^{-1} s^{-1} MPa^{-1}] were found between trees of high siltation sites with trees of low siltation sites (*Avicennia* (am): U= 43, p>0.05; *Avicennia* (pm): U= 49, p>0.05; *Rhizophora* (am): U = 37, p>0.05; *Rhizophora* (pm): U=27, p<0.1). However, small difference in stem conductance can be noticed between the two studied species. Whereas in *Avicennia marina*, the average specific stem conductance varies around 1.4 $x10^3$ mmol m^{-1} s^{-1} MPa^{-1}, *Rhizophora mucronata* has a higher average value varying around $2.4x10^3$ mmol m^{-1} s^{-1} MPa^{-1}. Striking is the difference in variability of the data, which turns out to be 3 times higher for *Rhizophora mucronata* measurements compared to the variability for *Avicennia marina*.

During the experiment it was remarkable that the flow of the loading dye sometimes appeared to happen into the opposite direction, namely towards the pressure head. This phenomenon occurred slightly more within branches of silted trees (Fig 3.13). Especially silted *Rhizophora mucronata* trees sampled in the morning, seems to be more subjected to opposite flow direction. This results in a small, however insignificant (U=27, p<0.1), difference in specific stem conductance between branches of silted *Rhizophora* trees sampled in the morning (am) and those sampled in the afternoon (pm).

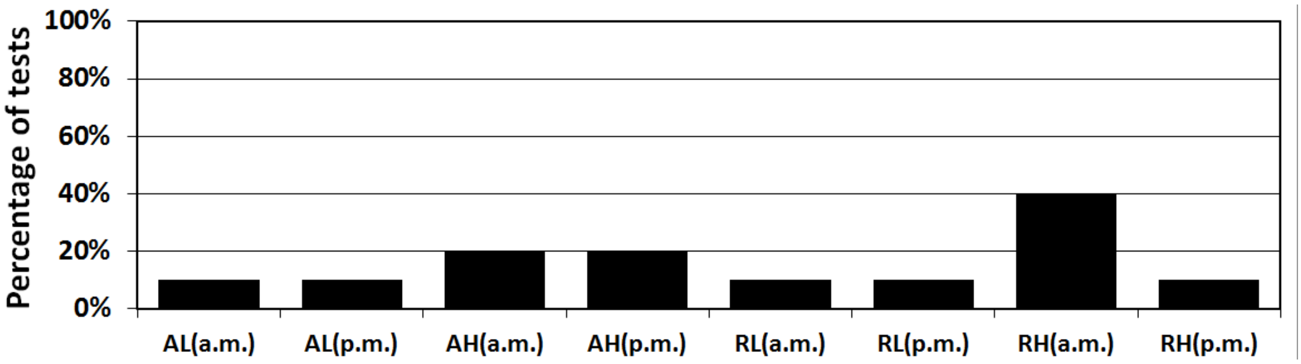


Figure 3.13. Percentage of tested branches in which in an opposite flow direction appeared. AL, AH, RL and RH respectively represent *Avicennia* in low siltation, *Avicennia* in high siltation, *Rhizophora* in low siltation and *Rhizophora* in high siltation sites respectively. (a.m.) sampling in the morning; (p.m.) sampling in the afternoon. n = 10.

3.4Root characteristics

A significantly ($p<0.01$) higher number of crab holes with a diameter below 1cm was found underneath mangrove trees standing in low siltation substrate *Avicennia* (Table 3.3). The same trend was observed for *Rhizophora* trees, although it was not significant.

The number of pen roots and their respective height is lower in the silted sites (Table 3.4). The number of pen roots was significantly different ($p<0.05$) for roots with a length between 5 and 10 cm. When no distinction was made in height classes, a significantly ($p<0.05$) lower number of pen roots of *Avicennia* trees was found in the high siltation site.

Table 3.3. Median number of crab burrows per 0.25m² counted below the *Avicennia marina* and *Rhizophora mucronata* trees located within high siltation (H) and low siltation (L) sites. Crab burrows counted were smaller (<1) or bigger (≥) then 1 cm in diameter. n = 15.

Number of Crab holes /0.25m²	***Avicennia***		***Rhizophora***	
	L	**H**	**L**	**H**
<1	28 ± 13	22 ± 9*	52 ± 83	33 ± 25
≥1	13 ± 4	14 ± 7	9 ± 3	10 ± 4

Table 3.4. Median number of pen roots per 0.25 m² counted below *Avicennia marina* trees located within high siltation (H) and low siltation (L) sites. Pen roots are subdivided in groups according to their length. Statistical significant differences ($p<0.05$) are indicated by an asterisk

Number of pen roots per length class (cm)	***Avicennia***	
	L	**H**
[0-5[	8 ± 15	1 ± 15
[5-10[	4 ± 6	1 ± 2*
[10-15[	1 ± 2	0 ± 4
[15-20[	1 ± 2	0 ± 2
[20-25[	0 ± 1	0 ± 1
[25-30[	0 ± 1	0 ± 0

CHAPTER 4

4 Discussion

4.1 Division in low and high siltation site is justified

The soil sampling campaign indicated that the degree of siltation within the high siltation site is indeed higher than in the low siltation site. This can be stated since an extra 10 cm thick layer was found in the high silted site. The higher fraction of salt indicate that most of the sediment finds its origin by marine sediments. This higher fraction of salt is the reason why higher values of dissolved oxygen and redox were found. The texture of these soils provide more space for oxygen, but they will have a lower ability to retain water. Salt and nutrients will therefore percolate through this layer and will accumulate on the underlying soil layer. This explains de phenomena of the nutrients.

4.2 Siltation produces physiological stress in mangrove trees

A good definition of what is meant by ‘negative influences’ is necessary to answer the question: does siltation results in a negative influence on the performance of a mangrove tree? When abiotic and/or biotic parameters cause a shift in the environmental characteristics toward less favourable conditions, one may say that the tree is stressed when the tree performance declines compared with the former state (Lichtenthaler, 1998). Environmental changes will not automatically negatively influence the tree performance, because trees have the ability to change their anatomy or physiology. Due to these changes, they attempt to survive and cope with the altered environment by minimising fluctuations in tree performance (Chaves *et al.*, 2009; Lintunen *et al.*, 2010). When the adaptations of an organism are no longer sufficient to avoid fluctuations, one indicates these parameters to have a negative influence on the trees. The degree of performance is reflected by the photosynthetic activity and growth of the tree (Ball *et al.*, 1984). During this research, hydraulic conductivity and stomatal conductance were measured, since a decrease in these parameters would indicate the negative influence of siltation on the trees.

4.2.1 Stomatal conductance

Stress of mangrove trees is caused by water stress, drought, elevated CO_2, salt concentration, pollution and, recently proposed, the degree of siltation (Ellison, 1998; Abuodha *et al.*, 2001; Vaiphasa *et al.*, 2007; Reef *et al.*, 2010). Stomatal conductance is positively correlated with photosynthetic activity (a decrease in conductance will cause a decrease in photosynthesis rate) and is therefore an indirect indicator of the tree performance (Sanchez *et al.*, 2003) and opposed stress levels (Scholander *et al.*, 1962; Ball *et al.*, 1984; Brugnoli *et al.*, 1991; Hamerlynck *et al.*, 2000; Sobrado, 2000; Lawlor, 2002; Wullschleger *et al.*, 2002; Stepien *et al.*, 2006; Hao *et al.*, 2010; Naz *et al.*, 2010). Hence, the presence of a negative influence causing stress is registered by lower values of stomatal conductance (Franks *et al.*, 2001; Rahnama *et al.*, 2010).

Within this study, the stomatal leaf conductances of two mangrove trees (*Avicenannia marina* and *Rhizophora mucronata*) are compared when the trees were standing in high and low silted sites (Fig 3.6 and Fig 3.8). The results indicate that a higher stomatal conductance (mmol m^{-2} s^{-1}) mostly occurred in trees standing in the low silted sites compared to the high silted sites. This suggests that silted soils increase stress for a tree since lower stomatal leaf conductances have been correlated with higher environmental stress (Anyia *et al.*, 2004).

The accuracy of the performed stomatal conductance measurements by the AP4 porometer should be interpreted by caution, since calibration was performed only once before the measuring campaign due to technical restrictions. In addition, the relative humidity during calibration (40%) was significantly lower compared to the relative humidity during the field measurements (daily fluctuations between 55% up to 90%). As such, caution has to be taken when the absolute values of stomatal conductance are interpreted for this experiment. However, because this is a comparison study, the measurement error was equal for both plots. Therefore, differences between both sites can still be correctly interpreted, resulting in reliable conclusions as long as no absolute values are interpreted.

The daily pattern of stomatal conductance of *Avicennia marina* trees describes a relatively peculiar trend (Fig 3.6), deviating of what is addressed as a ‘normal’ pattern. Such a ‘normal’ pattern is observed for *Rhizophora mucronata*. A ‘normal’ pattern of stomatal conductance, for well-nourished C3-plants is clock shaped, conform to the pattern of solar radiation and vapour pressure deficit (Fig 4.1) (Brodribb *et al.*, 2004). In the morning, low initial values are expected due to the absence of sunlight and therefore also the absence of photosynthesis. When a high evaporation causes water stress within a tree, a dip can occur in this pattern (Fig 4.1). For some trees, even a succession of such dips can occur in the stomatal conductance pattern, this phenomenon is known as stomatal oscillation (Barrs, 1971; Steppe *et al.*, 2006). The stomatal conductance pattern of *Rhizophora mucronata* (Fig 3.8) shows a similar dip between 9h00 and 13h30, caused by closing stomata to protect the leaves from losing too much water due to transpiration.

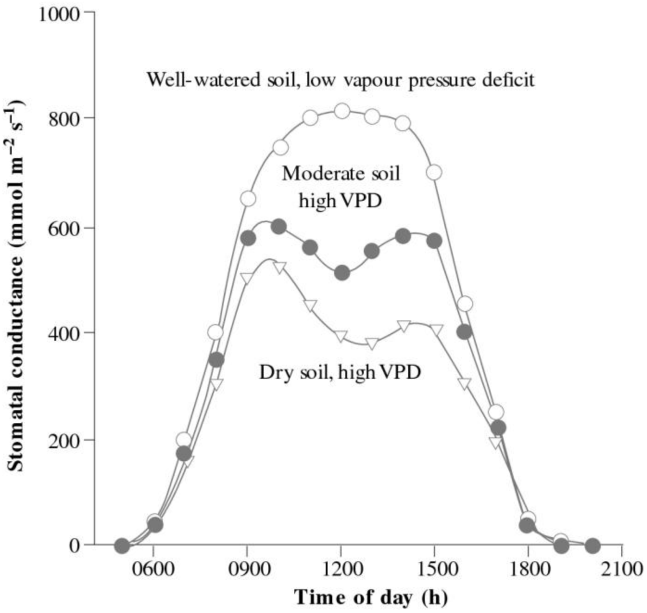


Figure 4.1: Each morning, prior to maximum daily irradiance on well-nourished C3-plants, the stomatal conductance increases rapidly. The stomata of unstressed plants remain open all day although a small dip is often observed when light and temperature reach theirs maximum and cause water loss by transpiration (Generalised values compiled by D. Eamus) (http://plantsinaction.science.uq.edu.au/edition1//?q=node/449#772)

Avicennia marina had high stomatal conductances for all early measurements (Fig 3.6). This is unlikely in C_3-plants and is considered as a more common characteristic for CAM plants (Herppich, 1997). Therefore, it can be hypothesised that *Avicennia marina*, which is a C_3 plant, imitates some typical CAM characteristics in an attempt to cope with the harsh environment. Another hypothesis is suggested by Hoste (2011a). He observed a similar pattern in *Avicennia marina* trees standing in a mangrove forest in Australia and attributed these findings to an opposite water flow (from leaves to roots). This opposite flow occurred during the night and rainfalls and is possibly linked to hydraulic redistribution. As such, the high values for stomatal conductance we observed in the morning in *Avicennia marina* trees suggest an opposite water flow resulting from water uptake of dew which is condensed on the leaves in the early morning. Considering mangrove trees which are subjected to an environment with a low input of fresh water, all possible ways of fresh water uptake can be considered as a mayor advantage for the tree. Hence, the opposite flow direction, suggested by Hoste (2011b), can possibly be attributed to the uptake of dew through stomata which is then further relocated within the tree and transported towards the rhizosphere. This hypothesis is very plausible since research has indicated that for *Swietenia macrophylla* (Meliaceae) seeds the stomata were responsible for the uptake of water (Paiva *et al.*, 2006). This dew uptake is probably driven by the osmotic gradient formed by the high salinity of sap within the leaves. In addition, trees subjected to stress have a higher water demand than non-stressed trees. Therefore, the stressed *Avicennia marina* trees in the high silted site have higher stomatal openings in an attempt to increase the water uptake in the early morning when transpiration rate is still low (Fig 3.6). From the moment transpiration increases, stomata will close rapidly to avoid water loss. The reflex of closing stomata is slower for trees which are situated in more favourable conditions, namely the less silted site. It seems that the uptake of fresh water and the fast closure of the stomata is of vital importance for the stressed *Avicennia marina* trees in the high silted sites, as water uptake by other pathways is probably reduced. Hence, the uptake of dew by the leaves seems therefore a plausible explanation for the high stomatal conductance in *Avicennia marina* trees.

The correlation between air vapour pressure deficit and leaf stomatal conductance for both sites (Fig 3.7) confirms the less pronounced stomata-closing reflex trees in low silted sites compared to high silted sites. When the vapour pressure deficit of the air increased, or in other words more water was lost by transpiration, it resulted in a faster closure of the leaf stomata in the high silted plots to avoid further water losses.

4.2.2 Hydraulic conductivity

Because no significant differences were found in hydraulic conductivity between sites, it seems that both tree species adapted anatomical and/or physiolocal to assure a constant hydraulic conductivity independent to the siltation degree of the soil. A difference however has found in stem conductance between both species, with higher values for *Rhizophora*. The lower variability in hydraulic conductance for *Avicennia marina* compared to *Rhizophora mucronata* can result from the fresh water hydraulic redistribution towards the rhizosphere. It seems that *Avicennia* trees can therefore better fine regulate their sap flow during the day since they have diluted the salt soil water resulting in lowered water potentials needed for the uptake of water by the roots. During the day they can easily tap water from these reservoir making the variability in hydraulic conductance more gradual. Another possibility is perhaps a better regulation of this sap flow due to the higher percentage of the cross section area that is confiscated by xylem (Fig 3.10). This again forms a reservoir of water which can be used in periods of need, making fluctuations more gradual.

During the hydraulic conductivity experiment, trees originating from high silted sites resulted more in opposite flow directions (Fig 3.13). This phenomenon is most likely caused by dehydrated cells which have an urgent need for water to restore the osmotic gradient and the turgor pressure within the cells. In normal situations, this demand is satisfied by upwards transport of water. However, when dehydration reaches a flip over point in osmotic potential, cells will suck water against normal flow direction, resulting in an opposite flow. Therefore, an opposite flow within branches is perhaps always present, but probably it is mostly lifted or hidden by the upwards water transport. Trees in high silted sites seems to have more dehydrated branch cells due to the higher stress rate, and as such more negative/opposite sap flows can occur. Within a tree, this higher suction gradient of dehydrated branch cells would result in a relocation of water in the leaves toward the cells in the branches. This process would support the dew uptake by the leaves.

Despite the ‘primitive’ character of the method for measuring hydraulic conductance, it should be mentioned that this method is able to measure opposite flow directions. Sap flow sensors, which are able to measure flow in both directions, only measure opposite sap flow rates when the upwards sap flow becomes less strong than the downward sap flow. Therefore, small opposite flows are difficult to measure with these sensors.

4.3 Anatomical adaptations to withstand the negative influence of siltation

Table 4.1 gives an overview of the tree characteristics that differ between high and low silted sites.

Table 4.1. Overview of changing tree characteristics with the degree of siltation. Arrows indicate an increase (↑) or decrease (↓) in values of the respective characteristic when measured within a silted plot, compared to trees in less silted plots. (=) precedes all characteristics that change in the same extent for both species. (≠) precedes characteristics that change, but they are specific per species.

Similar effects	*Avicennia marina*		*Rhizophora mucronata*	
=	Amount Of Leaves			↑
	Size Of Leaves			↓
	Water Content Leaves			↓
	Stomatal Area			↓
	Vessel-Leaf Correlation			↑
≠	Pore Area Index	↑		
	Stomata Density	↑		
	Phloem Area	↑		
	Vessel Area	↓		
			Total lumen area	↑
			Vessel Density	↑

4.3.1 Similar adaptations to siltation for *Avicennia* and *Rhizophora*

Avicennia marina and *Rhizophora mucronata* trees located in the highly silted plots have more, but smaller leaves (Fig 3.1). As previously discussed, siltation results in water stress leading to a change in leaf size and number (Heckenberger *et al.*, 1998; Schurr *et al.*, 2000; Anyia *et al.*, 2004; Burghardt *et al.*, 2008). Smaller leaves assure less loss of water by transpiration since they enhance the heat transfer rate resulting in less transpiration (Quarrie *et al.*, 1977; Ball, 1988a; Brugnoli *et al.*, 1991; Naidoo, 2010). A higher amount of small leaves is also favourable when environmental conditions are too demanding and leaf shedding is caused (Gu *et al.*, 2007). Energy withdrawal out of these leaves and the eventual senescence of the leaves is indeed better fine regulated when more smaller leaves are present. This adaptation can consequently be seen as an attempt by the tree to cope with a harsher environment, to regulate water loss by transpiration and to fine regulate potential energy losses due to leaf senescence.

The leaf water content was higher within leaves of less silted mangrove trees. This effect was less pronounced for *Avicennia marina* and more striking for *Rhizophora*. Probably the larger *Rhizophora* leaves have a higher ability to store water compared to the smaller *Avicennia* leaves (Fig 3.2a,b). The higher leaf water content of less silted trees is caused by the lower water stress conditions related to the lower degree of siltation. Hence, these trees have the ability to store more water in their leaves. In contrast, trees in high silted sites have more water stress which probably reduces the water potential in their leaves and causes the lower water content. Water will not reach the leaves since due to closed stomata, hydraulic conductivity stops. No water delivery by sap will cause other tissue to dry out which creates an osmotic gradient, which will result in a sucking force on the reservoirs of the leaves causing depletion of leaf water content. The higher amount of water stress in highly silted sites will obstruct trees to store an equally amount of water in the leaves compared to the less silted sites which have a better water supply (Scholz *et al.*, 2007).

Promising results were found when the total leaf area was compared with the vessel area (Fig 3.3), although for future research a higher amount of samples is advisable. A high correlation (r^2-value) was found between vessel area and total leaf area per branch for mangrove trees within highly silted sites. This correlation was absent for trees located in less silted sites. Hence, it seems that the trees impose a more strictly vascular arrangement when they are subjected to harsher stress conditions probably to avoid cavitation (Lintunen *et al.*, 2010). When this stress factor declines these mangrove trees seem to allow more freedom in their internal regulation. *Rhizophora* in low silted sites contained an outlier. Removal of this point will result in a linear correlation with a high r^2-value. However, intensive investigation of the database does not indicate that this value as wrong, Therefore, this measure was not removed and taken into account in this study.

The last common adaptation for *Rhizophora mucronata* and *Avicennia marina* is the lower stomatal area noticed in highly silted sites (Fig 3.4b,e). Similar to the smaller leaves, this phenomenon can be addressed as a strategy of the tree to cope with the higher stress level caused by the higher siltation degree. According to many scientists (Franks *et al.*, 2001; Franks *et al.*, 2009a; Franks *et al.*, 2009b; Naz *et al.*, 2010), the presence of smaller stomata results in an advantage for trees handling water stress, since they have a faster response time, lose less water and have better water-use efficiencies (Franks *et al.*, 2009a). This fast closure reflex of the stomata is related to the smaller guard cells that can change osmotic and turgor pressure more quickly (Franks *et al.*, 2009b).

4.3.2 Species specific adaptations to siltation for *Avicennia*

Plants adapt to buffer any slight alteration in the physiological processes that regulate the tree performance. *Avicennia marina* is no exception in this matter. One of the most striking anatomical adjustments is the increase in stomatal density (Fig 3.4a). which also has been reported in other research where stressed mangroves were examined (Heckenberger *et al.*, 1998; Franks *et al.*, 2001; Sobrado, 2007; Hameed *et al.*, 2008; Franks *et al.*, 2009a). The combination of smaller stomata and a higher stomatal density results in an better fine regulation of water loss and is positive for the water-use efficiency. In contrast, Hameed *et al.* (2008) observed a lower stomatal density in salinity stressed cogon grass (*Imperata cylindrical* L.) located in Faisalabad. They explained the lower density as feature to reduce the water loss through the leaf surface.

In addition, the higher stomatal density can be related to the previously discussed hypothesis of stomatal water uptake. The higher density results in a higher number of stomata that can contribute to the fresh water uptake from dew. Hence, this density cancels out the negative effect of the smaller stomata which have a higher resistance to the stomatal water uptake (even though smaller stomata are positive for fine regulating the water loss by transpiration). The higher pore area index in the highly silted sites confirms this assumption. As such, it can be hypothesized that trees in silted sites would dependent more on the stomatal water uptake from dew and have thus a higher pore area per leaf area to permit a faster and higher water uptake by stomata .

This study revealed a decreased vessel area in trees grown in the highly silted plots compared to trees grown in the less silted sites (Fig 3.11c). This finding confirms the increase of water stress level with the degree of siltation. When the water stress level rises, the probability of embolism simultaneously increases. When vessels are filled with air, they lose their ability to transport sap and form a barrier in the sap transport chain. Embolism is therefore not desirable, a high amount of embolised vessels can in the worst case even cause tree mortality. For this reason, trees try to protect themselves against this phenomenon using different possible adaptations. The formation of vessels with a smaller area is often observed when stress rises (Logullo *et al.*, 1995; Villagra *et al.*, 1997; Arnold *et al.*, 1999; Corcuera *et* *al.*, 2004; Mauseth *et al.*, 2004; Stevenson *et al.*, 2004). Smaller vessels can withstand more stress before embolism sets in (Sobrado, 2007; Hao *et al.*, 2010), because they have a smaller wall area which results in a relative low pit area per vessel and hence a lower risk on cavitation (Choat *et al.*, 2005; Hacke *et al.*, 2006; Sobrado, 2007). De Boer and Volkov (De Boer *et al.*, 2003) proposed another hypothesis: the large surface-to-volume ratio of vessels with small diameters would enhance the control the xylem sap composition. *Avicennia mucronata* trees will thus reduce the chance of embolism by forming smaller vessels which can endure higher stress levels caused by the increased degree of siltation.

A higher phloem ratio was found in highly silted sites for *Avicennia* trees (Fig 3.11a). This behaviour is known as a stress adaptation in *Avicennia marina* (Robert *et al.,* 2011a) and other species (Hameed *et al.*, 2008). Since siltation causes water stress and increases, as such, the risk of cavitation, the higher phloem ratio is possibly related to a mechanism which reduces the risk of embolism (Zwieniecki *et al.*, 2000; Salleo *et al.*, 2004; Salleo *et al.,* 2006). The phloem tissue is thought to be involved in the repair of cavitated vessels: the phloem tissue releases substances in the cavitated vessels creating a radial osmotic flow into the embolized conduits (Zwieniecki *et al.*, 2000).

4.3.3 Species specific adaptations to siltation for *Rhizophora*

When the soil is silted, *Rhizophora* trees do not invest in stomatal adaptations like *Avicennia* trees do (Fig 3.4). The anatomical features of *Rhizophora* trees (Fig 3.12) indicate that these trees change the anatomical structure of their vessels in response to siltation. In contrast to *Avicennia*, *Rhizophora* trees do not decrease the vessel area, instead these trees increase their total vessel density (Fig 3.12a). This behaviour was previously reported by Schmitz *et al.* (2006) (Fig 4.2) and they attributed this behaviour to a strategy called ‘conductive safety’ which reduces the risk of caviation. Indeed, more vessels per cross section area create a higher amount of potential transport routes from the roots up to the leaves. As such, a larger proportion of the vessels remainsfunctional when a fixed number of vessels is embolized (Baas *et al.*, 1983; Mauseth *et al.*, 1997; Villar-Salvador *et al.*, 1997; Mauseth *et al.*, 2004; Robert *et al.,* 2009). In addition, this adaptation increases the sap flow through the tree when no embolism is present resulting in a higher capacity of water storage during periods when the water supply is not limited. Due to the higher vessel density, the total lumen area increases with the siltation degree (Fig 3.11,d and 3.12,c).

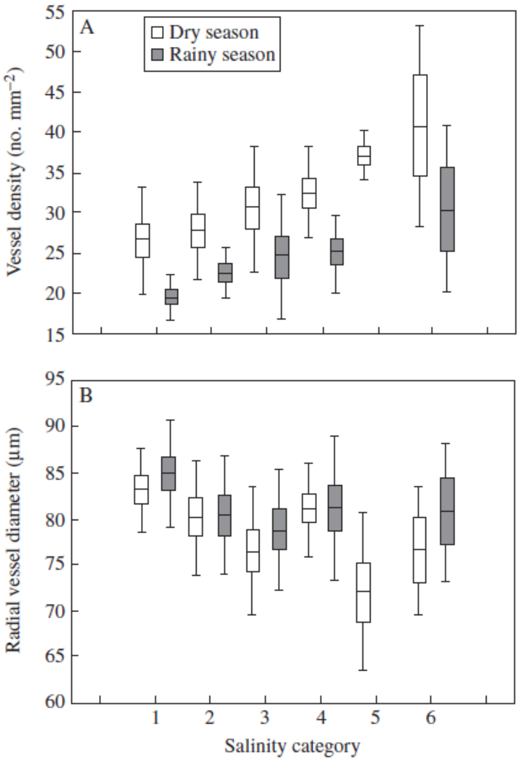


Figure 4.2. Vessel density and radial vessel diameter in function of salinity stress which is subdivided in six categories (Schmitz *et al.,* 2006).

4.4 Root characteristics

The most plausible explanation for the presence of fewer small crab burrows in the high siltation site (Table 3.3), is that small crabs must experience difficulties for digging due to the soil texture (Frusher *et al.*, 1994). It appears that bigger crabs do not have such difficulty upon a higher degree of siltation. If siltation indeed causes a decrease of crab burrows, this would indirectly effect the aeration of the soil. This indirect parameter of soil aeration results in more stressful conditions when this parameter declines.

During the counting of the number of pen roots of *Avicennia marina*, we observed a lower amount of pen roots in the high siltation sites. The cause for this phenomenon is still unclear. Perhaps there are on average an equal number of pen roots, of which most of them are buried due to siltation, or the survival conditions and higher stress of the environment for trees in silted area is reducing the formation of pen roots. However, since pen roots are of vital interest for the performance of a tree, one may assume that a lower number of these pen roots reflects a lower health condition of the tree. This again forms a indication of the negative influence by siltation

CHAPTER 5

5 Conclusions and perspectives

5.1 Conclusions

First goal of this research was to indicate whether siltation causes a negative effect on mangrove trees and secondly, the question rose if anatomical and/or physiological characters were influenced by sedimentation. What in turn can also indicate stress induced by siltation since trees will try to temper fluctuations in their performance by adaptations as their anatomical and/or physiological characteristics.

For the measurement campaign, many standardizations and measurements of biotic and abiotic characteristics were taken, assuring that within this mangrove ecosystem the degree of siltation causes the degree of stress. Indicating a difference in siltation was obtained by soil sampling, habitus characteristics, the colour of the sand, the steepness of de hill slope and the distance toward the ocean. When combining all these parameters, one may indeed indicate two regions of which one is high siltation and the other one is low siltation. (see section 4.3.2).

A decrease in stomatal conductance and hydraulic conductance may result from a tree which can no longer adapt itself to the negative influence of stress, since the tree does not succeed in avoiding fluctuations in performance. For *Avicennia marina* as well as for *Rhizophora mucronata*, we observed a lower diurnal pattern in stomatal conductance for the trees in the high siltation sites. This observation indicate that a higher degree of siltation indeed imposes a higher factor of stress on a tree, influencing it negatively since the lower stomatal conductance indicate lower capacity for photosynthesis. At first sight there was no decrease or difference in hydraulic conductance between both species when high siltation sites were compared with low siltation sites. But when comparing the directions of the flow of loading dye within the experiments, we observed more opposite flow directions within the high siltation sites. This phenomenon was presumably caused by the higher amount of dehydrated cells within branches of high siltation plots and therefore it may be an indicator of higher water stress when siltation increases.

The daily pattern of stomatal conductance for *Avicennia marina* deviates from what is generally accepted as normal. The stomatal conductance is linked with a water use efficiency of the tree, closing the stomata during most of the day, avoiding water loss by transpiration. The high initial values of the measurement days were according to the suggested hypothesis linking the influx of fresh dew water during the night. This hypothesis was built on previous research where negative sap flows were indicated for *Avicennia marina* at night and after rain fall. The osmotic gradient build up by the salinity within sap flow of *Avicennia* might drive the transport of dew from the outside of the leaf towards the internal leaf tissue.

Anatomical differences were observed between highly and less silted sites, of which some were observed in both *Avicennia marina* and *Rhizophora mucronata*, while others were species specific. Adaptations that were found in both species were an increase in the number of leaves, while the average leaf size became smaller. Aside from this, the stomatal area was significantly lower for high siltation sites. All previous mentioned characteristics are found to be known as an attempt of trees and plants to cope with higher stress and to assure a better water-use efficiency. A more strictly regulated leaf-vessel relation indicate the higher amount of stress causing the trees to lose their luxury of anatomical freedom. The lower water content in leaves in high siltation plots is a result of the lower water availability and thus the ability of storing water in the leaves.

Anatomical changes in *Avicennia marina* trees indicated that this species opt for anatomical adaptations of the stomata. Stomatal density and pore area index increased as a known measure to increase the water use efficiency of the tree. Since stress corresponds with a higher chance on cavitation of the vessels, adaptations hindering or decreasing the chance of the set in of embolism would therefore be of mayor importance for trees subjected to higher stress. Smaller vessel area and a higher phloem ratio are common knowledge of protecting trees against cavitation. Both adaptations were observed within the high siltation trees and thus form another indication of the higher stress by siltation and the attempt of the tree to cope with this less favourable environment.

For *Rhizophora mucronata*, anatomical adaptations were more directed towards changes in vessel anatomy. An increase in vessel density and total lumen area was found within trees standing in the high siltation plots. This adaptation again forms a protective adaptation to cope with higher chances of cavitation caused by higher stress originating from higher degree of siltation. More vessels forming the hydraulic architecture of the tree correspond with a higher amount of transport routes for water flow and thus decrease the impact of cavitation.

The amount of crab burrows were lower within the high siltation site, resulting in less aeration within the soil and thus resulting in an additional stress factor for the trees. Especially small crab burrows were decreased, probably by the change in soil texture hindering the small crabs. The number of pen roots of *Avicennia marina* were also observed to be lower, which can be the result of burying capacity of siltation. Less pen roots means coping with a decreased uptake of oxygen, indicating higher stress for the trees.

5.2Perspectives

For further research, it would be interesting to verify the hypothesis of uptake of dew water by the leaves, revealing the link between high stomatal conductance in the early morning and the reverse sap flow from branches toward the rhizosphere. This can be proven for instance by adding a traceable liquid within the dew, so the uptake within the tree would easily be seen. On the other hand, it would be interesting to examine if trees under stress can absorb water through their leaves. Are the stomata, if not the trichomes, indeed responsible for the uptake of water, or are other pathways used for the water uptake? As a proposal, a setup under a controlled environment, can be made containing trees of different degree of water deficit. Close examination of what happens with the stomata if leaves are moistened and study of the dew water will result in valuable knowledge.

Another question rising is whether salt excretion by the salt glands of *Avicennia* leaves, which also occurs in the early morning, might be linked with the intake of dew through stomata. Is this indeed linked with each other, and what is the exact mechanism? Does the osmotic gradient, formed by the salt content of the xylem sap, cause the withdrawal of water from the outer side of the leaf, through the stomata or trichomes? At which point in time do the leaves secret their salt? Do the leaves increase their internal salt concentration as a tool to increase the osmotic gradient and with it increase the capacity of water uptake by dew? Is salt secretion combined with a closure of the stomata, when the advantage of water uptake is cancelled out by transpiration, so internal salt increase would not have additional use? Further research can verify this and can give an answer on what the exact advantage is of salt excretion of the leaves for the uptake of dew.

In general, using a controlled environment instead of measurements in the field would be of high value for research towards the effect of siltation on mangroves, since other biotic and abiotic parameters can be controlled. This would also create opportunities to examine at which exact degree of siltation, a mangrove tree starts to encounter negative effects on tree performance. This information is of importance for the rehabilitation of mangroves in silted areas and may cause better regulations for dredging disposal.

CHAPTER 6

6 References

Abuodha, P.A.W. & Kairo, J.G. (2001). Human-induced stresses on mangrove swamps along the Kenyan coast. *Hydrobiologia*, ***458***, 255-265.

Allingham, D.P. & Neil, D.T. (1995). The supratidal deposits and effects of coral dredging on mud island, Moreton Bay, Southeast Queensland. *Zeitschrift Fur Geomorphologie*, ***39***, 273-292.

Alongi, D.M. (2002). Present state and future of the world's mangrove forests. *Environmental Conservation*, ***29***, 331-349.

Alongi, D.M. (2008). Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine Coastal and Shelf Science*, ***76***, 1-13.

Alongi, D.M., Pfitzner, J., Trott, L.A., Tirendi, F., Dixon, P. & Klumpp, D.W. (2005). Rapid sediment accumulation and microbial mineralization in forests of the mangrove Kandelia candel in the Jiulongjiang Estuary, China. *Estuarine Coastal and Shelf Science*, ***63***, 605-618.

Angeles, G., Lopez-Portillo, J. & Ortega-Escalona, F. (2002). Functional anatomy of the secondary xylem of roots of the mangrove Laguncularia racemosa (L.) Gaertn. (Combretaceae). *Trees-Structure and Function*, ***16***, 338-345.

Anyia, A.O. & Herzog, H. (2004). Water-use efficiency, leaf area and leaf gas exchange of cowpeas under mid-season drought. *European Journal of Agronomy*, ***20***, 327-339.

APHA (1998). *Standard method for the examination of water and waste-water*. (20th ed.).

Arnold, D.H. & Mauseth, J.D. (1999). Effects of environmental factors on development of wood. *American Journal of Botany*, ***86***, 367-371.

Ashton, E.C., Hogarth, P.J. & Ormond, R. (1999). Breakdown of mangrove leaf litter in a managed mangrove forest in Peninsular Malaysia. *Hydrobiologia*, ***413***, 77-88.

Baas, P., Werker, E. & Fahn, A. (1983). Some ecological trends in vessel characters. *Iawa Bulletin*, ***4***, 141-159.

Ball, M.C. (1980). Patterns of secondary succession in a mangrove forest of Southern Florida. *Oecologia*, ***44***, 226-235.

Ball, M.C. (1988a). Ecophysiology of mangroves. *Trees-Structure and Function*, ***2***, 129-142.

Ball, M.C. (1988b). Salinity tolerance in the mangroves Aegiceras-corniculatum and Avicennia-marina.1. water-use in relation to growth, carbon partitioning, and salt balance. *Australian Journal of Plant Physiology*, ***15***, 447-464.

Ball, M.C. & Anderson, J.M. (1986). Sensitivity of photosystem-II to NaCl in relation to salinity tolerance - comparative - studies with thylakoids of the salt - tolerant mangrove, Avicennia-marina, and the salt_sensitive pea, Pisum sativum. *Australian Journal of Plant Physiology*, ***13***, 689-698.

Ball, M.C. & Farquhar, G.D. (1984). Photosynthetic and stomatal responses of 2 mangrove species, Aegiveras corniculatum and Avicennia marina, to long-term salinity and humidity conditions. *Plant Physiology*, ***74***, 1-6.

Barrs, H.D. (1971). cyclic variations in stomatal aperture, transpiration, and leaf water potential under constant environmental conditions. *Annual Review of Plant Physiology*, ***22***, 223-&.

Blasco, F. & Aizpuru, M. (2001). Depletion of mangroves of continental Asia. *Wetlands Ecol Manag*, ***9***, 245-256.

Boto, K.G. & Wellington, J.T. (1984). Soil characteristics and nutrient status in a Northern Australian mangrove forest. *Estuaries*, ***7***, 61-69.

Brodribb, T.J. & Holbrook, N.M. (2004). Diurnal depression of leaf hydraulic conductance in a tropical tree species. *Plant Cell and Environment*, ***27***, 820-827.

Brokaw, N. & Thompson, J. (2000). The H for DBH. *Forest Ecology and Management*, ***129***, 89-91.

Brugnoli, E. & Lauteri, M. (1991). Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt-tolerant (Gossypium-hirsutum L) and salt-sensitive (Phaseolus-vulgaris L) C3 non-halophytes. *Plant Physiology*, ***95***, 628-635.

Burghardt, M., Burghardt, A., Gall, J., Rosenberger, C. & Riederer, M. (2008). Ecophysiological adaptations of water relations of Teucrium chamaedrys L. to the hot and dry climate of xeric limestone sites in Franconia (Southern Germany). *Flora*, ***203***, 3-13.

Cannicci, S., Burrows, D., Fratini, S., Smith, T.J., Offenberg, J. & Dahdouh-Guebas, F. (2008). Faunal impact on vegetation structure and ecosystem function in mangrove forests: A review. *Aquatic Botany*, ***89***, 186-200.

Carey, G. (1934). Further inverstigations on the embryology of viviparous seeds. *Proceedings of The Linnean Society of New South Wales*, ***59***, 392-410.

Chapman, V.J. (1976). *Mangrove vegetation*. th ed.): Leutershousen.

Chaves, M.M., Flexas, J. & Pinheiro, C. (2009). Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Annals of Botany*, ***103***, 551-560.

Choat, B., Lahr, E.C., Melcher, P.J., Zwieniecki, M.A. & Holbrook, N.M. (2005). The spatial pattern of air seeding thresholds in mature sugar maple trees. *Plant Cell and Environment*, ***28***, 1082-1089.

Choat, B., Medek, D.E., Stuart, S.A., Pasquet-Kok, J., Egerton, J.J.G., Salari, H., Sack, L. & Ball, M.C. (2011). Xylem traits mediate a trade-off between resistance to freeze-thaw-induced embolism and photosynthetic capacity in overwintering evergreens. *New Phytologist*, ***191***, 996-1005.

Choudhury, J.K. (1997). Mangroves and other coastal forests Sustainable management of mangroves, forest development and social needs. XI World Forestry Congress. Antalya, Turkey. **6:** 13-22.

Chu, H.Y., Chen, N.C., Yeung, M.C., Tam, N.F.Y. & Wong, Y.S. (1998). Tide-tank system simulating mangrove wetland for removal of nutrients and heavy metals from wastewater. *Water Science and Technology*, ***38***, 361-368.

Clarke, L.D. & Hannon, N.J. (1970). Mangrove swamp and salt marsh communities of Sydney district .3. plant growth in relation to salinity and waterlogging. *Journal of Ecology*, ***58***, 351.

Corcuera, L., Camarero, J.J. & Gil-Pelegrin, E. (2004). Effects of a severe drought on Quercus ilex radial growth and xylem anatomy. *Trees-Structure and Function*, ***18***, 83-92.

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

Davis, J.H. (1940). The ecology and geologic role of mangroves in Florida. *Carnegie Inst. Wash Pap. Tortugas Lab.*, ***517***, 305-412.

De Boer, A.H. & Volkov, V. (2003). Logistics of water and salt transport through the plant: structure and functioning of the xylem. *Plant Cell and Environment*, ***26***, 87-101.

De Ryck, D. (2009). *Moving and Settling: Experiments on the dispersal and establishment of hydrochorous propagules.* Biology, Vrije Universiteit Brussel, Brussel.

Drennan, P. & Pammenter, N.W. (1982). Physiology of salt excretion in the mangrove Avicennia-marina (Forsk) Vierh. *New Phytologist*, ***91***, 597-606.

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

Ellis, J., Nicholls, P., Craggs, R., Hofstra, D. & Hewitt, J. (2004). Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. *Marine Ecology-Progress Series*, ***270***, 71-82.

Ellison, A.M. & Farnsworth, E.J. (1996). Spatial and temporal variability in growth of Rhizophora mangle saplings on coral cays: Links with variation in insolation, herbivory, and local sedimentation rate. *Journal of Ecology*, ***84***, 717-731.

Ellison, J.C. (1998). Impacts of sediment burial on mangroves. *Marine Pollution Bulletin*, ***37***, 420-426.

Elmqvist, T. & Cox, P.A. (1996). The evolution of vivipary in flowering plants. *Oikos*, ***77***, 3-9.

Feller, I.C. & Sitnik, M., (Eds.) (1996). Mangrove Ecology: a Manual for a Field Course, Sithsonian Institution.

Finlayson, C.M. & Spiers, A.G. (1999). Global review of wetland resources and priorityies for wetland inventory. Supervising Scientist report 144. S. Scientist. Canberra.

Franks, P.J. & Beerling, D.J. (2009a). Maximum leaf conductance driven by CO2 effects on stomatal size and density over geologic time. *Proceedings of the National Academy of Sciences of the United States of America*, ***106***, 10343-10347.

Franks, P.J., Drake, P.L. & Beerling, D.J. (2009b). Plasticity in maximum stomatal conductance constrained by negative correlation between stomatal size and density: an analysis using Eucalyptus globulus. *Plant Cell and Environment*, ***32***, 1737-1748.

Franks, P.J. & Farquhar, G.D. (2001). The effect of exogenous abscisic acid on stomatal development, stomatal mechanics, and leaf gas exchange in Tradescantia virginiana. *Plant Physiology*, ***125***, 935-942.

Frusher, S.D., Giddins, R.L. & Smith, T.J. (1994). Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary - effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. *Estuaries*, ***17***, 647-654.

Gartner, H. & Nievergelt, D. (2010). The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia*, ***28***, 85-92.

Gautier, D., Amador, J. & Newmark, F. (2001). The use of mangrove wetland as a biofilter to treat shrimp pond effluents: preliminary results of an experiment on the Caribbean coast of Colombia. *Aquaculture Research*, ***32***, 787-799.

Gilman, E.L., Ellison, J., Duke, N.C. & Field, C. (2008). Threats to mangroves from climate change and adaptation options: A review. *Aquatic Botany*, ***89***, 237-250.

Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J. & Duke, N. (2011). Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, ***20***, 154-159.

Gopal, B. & Krishnamurthy, K. (1993). Wetlands of south Asia. Wetland of the world; Handbook of vegetation Science D.F. Whgham, D. Dykyjova and S. Henjny, Inventory Ecology and Management, 345-414.

Gordon, D.M. (1988). Disturbance to mangroves in tropical-arid Western-Australia - hypersalinity and restricted tidal exchange as factors leading to mortality. *Journal of Arid Environments*, ***15***, 117-145.

Gu, M., Rom, C.R., Robbins, J.A. & Oosterhuis, D.M. (2007). Effect of water deficit on gas exchange, osmotic solutes, leaf abscission, and growth of four birch genotypes (Betula L.) under a controlled environment. *Hortscience*, ***42***, 1383-1391.

Hacke, U.G., Sperry, J.S., Wheeler, J.K. & Castro, L. (2006). Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology*, ***26***, 689-701.

Hameed, M. & Ashraf, M. (2008). Physiological and biochemical adaptations of Cynodon dactylon (L.) Pers. from the Salt Range (Pakistan) to salinity stress. *Flora*, ***203***, 683-694.

Hamerlynck, E.P., Huxman, T.E., Loik, M.E. & Smith, S.D. (2000). Effects of extreme high temperature, drought and elevated CO2 on photosynthesis of the Mojave Desert evergreen shrub, Larrea tridentata. *Plant Ecology*, ***148***, 183-193.

Hao, G.Y., Jones, T.J., Luton, C., Zhang, Y.J., Manzane, E., Scholz, F.G., Bucci, S.J., Cao, K.F. & Goldstein, G. (2009). Hydraulic redistribution in dwarf Rhizophora mangle trees driven by interstitial soil water salinity gradients: impacts on hydraulic architecture and gas exchange. *Tree Physiology*, ***29***, 697-705.

Hao, G.Y., Sack, L., Wang, A.Y., Cao, K.F. & Goldstein, G. (2010). Differentiation of leaf water flux and drought tolerance traits in hemiepiphytic and non-hemiepiphytic Ficus tree species. *Functional Ecology*, ***24***, 731-740.

Hardin, G. (1968). TRAGEDY OF COMMONS. *Science*, ***162***, 1243-&.

Heckenberger, U., Roggatz, U. & Schurr, U. (1998). Effect of drought stress on the cytological status in Ricinus communis. *Journal of Experimental Botany*, ***49***, 181-189.

Herppich, W.B. (1997). Stomatal responses to changes in air humidity are not necessarily linked to nocturnal CO2 uptake in the CAM plant Plectranthus marrubioides Benth (Lamiaceae). *Plant Cell and Environment*, ***20***, 393-399.

Hogarth, P.J. (2007). *The biology of mangroves and seagrasses*. (2nd editionth ed.) New York, USA: Oxford University Press.

Hollins, S.E., Harrison, J.J., Jones, B.G., Zawadzki, A., Heijnis, H. & Hankin, S. (2011). Reconstructing recent sedimentation in two urbanised coastal lagoons (NSW, Australia) using radioisotopes and geochemistry. *Journal of Paleolimnology*, ***46***, 579-596.

Hoste, P. (2011a). *Ecophysiology of mangrove in Australia: Hydraulic functioning*. Faculteit Bio-ingenieurswetenschappen (LA), UGent, Gent.

Hoste, P. (2011b). *Ecophysiology of mangrove in Australia: Hydraulic functioning*. Faculteit Bio-ingenieurswetenschappen (LA), UGent, Gent.

Hutchings, P. & Seanger, P. (1987). *Ecology of Mangroves*. th ed.) St. Lucia: University of Queensland Press.

Jansen, S., Kitin, P., de Pauw, H., Idris, M., Beeckman, H. & Smets, E. (1998). Preparation of wood specimens for transmitted light microscopy and scanning electron microscopy. *Belgian Journal of Botany*, ***131***, 41-49.

Jimenez, J.A. & Sauter, K. (1991). Structure and dynamics of mangrove forests along a flooding gradient. *Estuaries*, ***14***, 49-56.

Jones, H.G. (1992). *Plants and microclimate*. (2ndth ed.) Cambridge: Cambridge University Press.

Kathiresan, K. (2011) Importance of Mangrove Ecosystem. *Journal.*,

Kathiresan, K. & Bingham, B.L. (2001). Biology of mangroves and mangrove ecosystems. Advances in Marine Biology, Vol 40. A.J. Southward, P.A. Tyler, C.M. Young and L.A. Fuiman. **40**, 81-251.

Kitaya, Y., Yabuki, K., Kiyota, M., Tani, A., Hirano, T. & Aiga, I. (2002). Gas exchange and oxygen concentration in pneumatophores and prop roots of four mangrove species. *Trees-Structure and Function*, ***16***, 155-158.

Komiyama, A., Ong, J.E. & Poungparn, S. (2008). Allometry, biomass, and productivity of mangrove forests: A review. *Aquatic Botany*, ***89***, 128-137.

Krauss, K.W., Lovelock, C.E., McKee, K.L., Lopez-Hoffman, L., Ewe, S.M.L. & Sousa, W.P. (2008). Environmental drivers in mangrove establishment and early development: A review. *Aquatic Botany*, ***89***, 105-127.

Kristensen, E. & Alongi, D.M. (2006). Control by fiddler crabs (Uca vocans) and plant roots (Avicennia marina) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. *Limnology and Oceanography*, ***51***, 1557-1571.

Lawlor, D.W. (2002). Limitation to photosynthesis in water-stressed leaves: Stomata vs. metabolism and the role of ATP. *Annals of Botany*, ***89***, 871-885.

Lee, S.Y. (1998). Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research*, ***49***, 335-343.

Lee, S.Y. (1999). Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function. *Australian Journal of Ecology*, ***24***, 355-366.

Lichtenthaler, H.K. (1998). The stress concept in plants: An introduction. Stress of Life: From Molecules to Man. P. Csermely. New York, New York Acad Sciences. **851**, 187-198.

Lintunen, A. & Kalliokoski, T. (2010). The effect of tree architecture on conduit diameter and frequency from small distal roots to branch tips in Betula pendula, Picea abies and Pinus sylvestris. *Tree Physiology*, ***30***, 1433-1447.

Logullo, M.A., Salleo, S., Piaceri, E.C. & Rosso, R. (1995). Relations between vulnerability to xylem embolism and xylem conduit dimensions in youg trees of Quercus-cerris. *Plant Cell and Environment*, ***18***, 661-669.

Lopez-Portillo, J., Ewers, F.W. & Angeles, G. (2005). Sap salinity effects on xylem conductivity in two mangrove species. *Plant, Cell & Environment*, ***28***, 1285-1292.

Lugo, A.E. & Clintron, G., (Eds.) (1975). The mangrove forests of Puerto Rico and their management. Proceedings of the International Symposium on Biology and Management of Mangroves. Gainesville, University of Florida.

Lugo, A.E. & Snedaker, S.C. (1974). The ecology of mangroves. Annual Reviews of Ecology and Systematics. **5:** 39-64.

Macnae, W. (1968). A general account of fauna and flora of mangrove swamps and forests in Indo-West-Pacific region. *Advances in Marine Biology*, ***6***, 73-&.

Matthijs, S., Tack, J., van Speybroeck, D. & Koedam, N. (1999). Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study. *Mangroves and Salt Marshes*, ***3***, 243-249.

Mauseth, J.D. & PlemonsRodriguez, B.J. (1997). Presence of paratracheal water storage tissue does not alter vessel characters in cactus wood. *American Journal of Botany*, ***84***, 815-822.

Mauseth, J.D. & Stevenson, J.F. (2004). Theoretical considerations of vessel diameter and conductive safety in populations of vessels. *International Journal of Plant Sciences*, ***165***, 359-368.

McKee, K.L. (1993). Soil physicochemical patterns and mangrove species distribution - reciprocal effects. *Journal of Ecology*, ***81***, 477-487.

McKee, K.L. (1995). Seedling recruitment patterns in a Belizean mangrove forest - effects of establishment ability and physicochemical factors. *Oecologia*, ***101***, 448-460.

McMillan, C. (1971). Environmental factors affecting seedling establishment of black mangrove on central Texas coast. *Ecology*, ***52***, 927-&.

Mimura, N., Yasuhara, K., Kawagoe, S., Yokoki, H. & Kazama, S. (2011). Damage from the Great East Japan Earthquake and Tsunami - A quick report. *Mitigation and Adaptation Strategies for Global Change*, ***16***, 803-818.

Moberg, F. & Ronnback, P. (2003). Ecosystem services of the tropical seascape: interactions, substitutions and restoration. *Ocean & Coastal Management*, ***46***, 27-46.

Mohamed, M.O.S., Neukermans, G., Kairo, J.G., Dahdouh-Guebas, F. & Koedam, N. (2009). Mangrove forests in a peri-urban setting: the case of Mombasa (Kenya). *Wetlands Ecology and Management*, ***17***, 243-255.

Moore, R.T., Miller, P.C., Albright, D. & Tieszen, L.L. (1972). COMPARATIVE GAS-EXCHANGE CHARACTERISTICS OF 3 MANGROVE SPECIES DURING WINTER. *Photosynthetica*, ***6***, 387-393.

Moore, R.T., Miller, P.C., Ehlering.J & Lawrence, W. (1973). SEASONAL TRENDS IN GAS-EXCHANGE CHARACTERISTICS OF 3 MANGROVE SPECIES. *Photosynthetica*, ***7***, 387-394.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T. & den Hartog, C. (2000). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine Coastal and Shelf Science*, ***51***, 31-44.

Naidoo, G. (2010). Ecophysiological differences between fringe and dwarf Avicennia marina mangroves. *Trees-Structure and Function*, ***24***, 667-673.

Naz, N., Hameed, M., Ashraf, M., Al-Qurainy, F. & Arshad, M. (2010). Relationships between gas-exchange characteristics and stomatal structural modifications in some desert grasses under high salinity. *Photosynthetica*, ***48***, 446-456.

Nickerson, N.H. & Thibodeau, F.R. (1985). Association between pore water sulfide concentrations and the distribution of mangroves. *Biogeochemistry*, ***1***, 183-192.

Nye, P.H. & Tinker, P.B. (1977). *Solute Movement in the Soil-root System*. th ed.) London: Blackwell Scientific Publications.

Paiva, E.A.S., Lemos, J.P. & Oliveira, D.M.T. (2006). Imbibition of Swietenia macrophylla (Meliaceae) seeds: The role of stomata. *Annals of Botany*, ***98***, 213-217.

Parida, A.K. & Jha, B. (2010). Salt tolerance mechanisms in mangroves: a review. *Trees-Structure and Function*, ***24***, 199-217.

Parsons, T.R., Maita, Y. & Lalli, C.M. (1984). *A manual of chemical and biological methods for seawater analysis*. (1st ed.th ed.) Oxford, New York: Pergamon Press.

Pezeshki, S.R., DeLaune, R.D. & Meeder, J.F. (1997). Carbon assimilation and biomass partitioning in Avicennia germinans and Rhizophora mangle seedlings in response to soil redox conditions. *Environmental and Experimental Botany*, ***37***, 161-171.

Pool, D.J., Snedaker, S.C. & Lugo, A.E. (1977). Structure of mangrove forests in Florida, Puerto-Rico, Mexico, and Costa-Rica. *Biotropica*, ***9***, 195-212.

Popp, M., Polania, J. & Weiper, M., (Eds.) (1993). Physiological adaptations to different salinity levels in mangrove. Towards the Rational Use of High Salinity Tolerant Plants. Dordrecht, Kluwer Academic Publishers.

Quarrie, S.A. & Jones, H.G. (1977). Effects of abscisic-acid and water stress on development and morphology of wheat. *Journal of Experimental Botany*, ***28***, 192-&.

Rabinowitz, D. (1978). DISPERSAL PROPERTIES OF MANGROVE PROPAGULES. *Biotropica*, ***10***, 47-57.

Rahnama, A., James, R.A., Poustini, K. & Munns, R. (2010). Stomatal conductance as a screen for osmotic stress tolerance in durum wheat growing in saline soil. *Functional Plant Biology*, ***37***, 255-263.

Rapp, A.O. & Behrmann, K. (1998). Preparation of wood for microscopic analysis after decay testing. *Holz Als Roh-Und Werkstoff*, ***56***, 277-278.

Reef, R., Feller, I.C. & Lovelock, C.E. (2010). Nutrition of mangroves. *Tree Physiology*, ***30***, 1148-1160.

Robert, E.M.R., Koedam, N., Beeckman, H. & Schmitz, N. (2009). A safe hydraulic architecture as wood anatomical explanation for the difference in distribution of the mangroves Avicennia and Rhizophora. *Functional Ecology*, ***23***, 649-657.

Robert, E.M.R., Schmitz, N., Boeren, I., Driessens, T., Herremans, K., De Mey, J., Van de Casteele, E., Beeckman, H. & Koedam, N. (2011a). Successive Cambia: A Developmental Oddity or an Adaptive Structure? *Plos One*, ***6***.

Robert, E.M.R., Schmitz, N., Okello, J.A., Boeren, I., Beeckman, H. & Koedam, N. (2011b). Mangrove growth rings: fact or fiction? *Trees-Structure and Function*, ***25***, 49-58.

Robertson, A.I. & Daniel, P.A. (1989). The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia*, ***78***, 191-198.

Ruwa, R.K. & Polk, P. (1986). Additional information on mangrove distribution in Kenya: some observations and remarks. *Kenya Journal of Sciences Series*, ***B 7***, 41-45.

Ruzin, S.E. (1999). *Plant microtechnique and microscopy*. th ed.) New York, USA: Oxford University Press.

Saenger, P. (2002). *Mangrove ecology, silvicurture and conservation*. th ed.) Dordrecht: Kluwer Academic Publishers.

Salleo, S., Lo Gullo, M.A., Trifilo, P. & Nardini, A. (2004). New evidence for a role of vessel-associated cells and phloem in the rapid xylem refilling of cavitated stems of Laurus nobilis L. *Plant Cell and Environment*, ***27***, 1065-1076.

Salleo, S., Trifilo, P. & Lo Gullo, M.A. (2006). Phloem as a possible major determinant of rapid cavitation reversal in stems of Laurus nobilis (laurel). *Functional Plant Biology*, ***33***, 1063-1074.

Sanchez, H.B., Lemeur, R., Van Damme, P. & Jacobsen, S.E. (2003). Ecophysiological analysis of drought and salinity stress of quinoa (Chenopodium quinoaWilld.). *Food Reviews International*, ***19***, 111-119.

Sansanayuth, P., Phadungchep, A., Ngammontha, S., Ngdngam, S., Sukasem, P., Hoshino, H. & Ttabucanon, M.S. (1996). Shrimp pond effluent: Pollution problems and treatment by constructed wetlands. *Water Science and Technology*, ***34***, 93-98.

Schmitz, N. (2004). *Houtanatomie van de mangrove Rhizophora mucronata Lamk. en de relatie met de omgeving. De betekenis van de vatendichtheid voor de veiligheid van het watertransportsysteem.* Biologie, Vrije Universiteit Brussel, Brussel.

Schmitz, N., Verheyden, A., Beeckman, H., Kairo, J.G. & Koedam, N. (2006). Influence of a salinity gradient on the vessel characters of the mangrove species Rhizophora mucronata. *Annals of Botany*, ***98***, 1321-1330.

Scholand, P.F., Bradstre, E.D., Hammel, H.T. & Hemmings, E.A. (1966). Sap concentrations in halophytes and some other plants. *Plant Physiology*, ***41***, 529.

Scholander, P.F., Hemmingsen, E., Garey, W. & Hammel, H.T. (1962). Salt balance in mangroves. *Plant Physiology*, ***37***, 722.

Scholander, P.F., Hemmingsen, E.A., Hammel, H.T. & Bradstreet, E.D.P. (1964). Hydrostatic pressure + osmotic potential in leaves of mangroves + some other plants. *Proceedings of the National Academy of Sciences of the United States of America*, ***52***, 119.

Scholander, P.F., Vandam, L. & Scholander, S.I. (1955). Gas exchange in the roots of mangroves. *American Journal of Botany*, ***42***, 92-98.

Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C. & Miralles-Wilhelm, F. (2007). Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant Cell and Environment*, ***30***, 236-248.

Schurr, U., Heckenberger, U., Herdel, K., Walter, A. & Feil, R. (2000). Leaf development in Ricinus communis during drought stress: dynamics of growth processes, of cellular structure and of sink-source transition. *Journal of Experimental Botany*, ***51***, 1515-1529.

Schwarzbach, A.E. & Ricklefs, R.E. (2000). Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. *American Journal of Botany*, ***87***, 547-564.

Sherrod, C.L., Hockaday, D.L. & McMillan, C. (1986). Survival of red mangrove, Rhizophora-mangle, on the gulf-of-Mexico coast of Texas. *Contributions in Marine Science*, ***29***, 27-36.

Sherrod, C.L. & McMillan, C. (1985). The distributional history and ecology of mangrove vegetation along the Northern gulf of Mexico coastal region. *Contributions in Marine Science*, ***28***, 129-140.

Shimony, C., Fahn, A. & Reinhold, L. (1973). Ultrastructure and ion gradients in salt-glands of Avicennia-marina (Forssk) Vierh. *New Phytologist*, ***72***, 27.

Smith, N.F., Wilcox, C. & Lessmann, J.M. (2009). Fiddler crab burrowing affects growth and production of the white mangrove (Laguncularia racemosa) in a restored Florida coastal marsh. *Marine Biology*, ***156***, 2255-2266.

Smith, T.J. (1987). Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology*, ***68***, 266-273.

Sobrado, M.A. (2000). Relation of water transport to leaf gas exchange properties in three mangrove species. *Trees-Structure and Function*, ***14***, 258-262.

Sobrado, M.A. (2007). Relationship of water transport to anatomical features in the mangrove Laguncularia racemosa grown under contrasting salinities. *New Phytologist*, ***173***, 584-591.

Sorrell, B.K., Mendelssohn, I.A., McKee, K.L. & Woods, R.A. (2000). Ecophysiology of wetland plant roots: A modelling comparison of aeration in relation to species distribution. *Annals of Botany*, ***86***, 675-685.

Spalding, M., R., B. & Field, C. (1997). *World Mangrove Atlas*. th ed.) Okinawa, Japan: The International Society for Mangrove Ecosystems.

Srivastava, J., Farooqui, A. & Hussain, S.M. (2012). Sedimentology and salinity status in Pichavaram mangrove wetland, South East coast of India, International Journal of Geology, Earth and Environmental Sciences. **2:** 7-15.

Steinke, T.D., Rajh, A. & Holland, A.J. (1993). The feeding-behavior of the red mangrove crab Sesarma-meierti-De Man, 1887 (Crustacea, Decapoda, Grapsidae) and its effect on the degradation of mangrove leaf-litter. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap*, ***13***, 151-160.

Stepien, P. & Klobus, G. (2006). Water relations and photosynthesis in Cucumis sativus L. leaves under salt stress. *Biologia Plantarum*, ***50***, 610-616.

Steppe, K. (2011). *Ecophysiologie*. th ed.) Gent: Faculteit Bio-Ingenieurswetenschappen, Universiteit Gent.

Steppe, K., Dzikiti, S., Lemeur, R. & Milford, J.R. (2006). Stomatal oscillations in orange trees under natural climatic conditions. *Annals of Botany*, ***97***, 831-835.

Sternberg, L.D.L. & Swart, P.K. (1987). Utilization of fresh-water and ocean water by coastal plants of Southern Florida. *Ecology*, ***68***, 1898-1905.

Sternberg, L.D.L., Teh, S.Y., Ewe, S.M.L., Miralles-Wilhelm, F. & DeAngelis, D.L. (2007). Competition between hardwood hammocks and mangroves. *Ecosystems*, ***10***, 648-660.

Stevenson, J.F. & Mauseth, J.D. (2004). Effects of environment on vessel characters in cactus wood. *International Journal of Plant Sciences*, ***165***, 347-357.

Stieglitz, T., Ridd, P. & Muller, P. (2000). Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. *Hydrobiologia*, ***421***, 69-76.

Stuart, S.A., Choat, B., Martin, K.C., Holbrook, N.M. & Ball, M.C. (2007). The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist*, ***173***, 576-583.

Taiz, L. & Zeiger, E. (2006). *Plant physiology*. (4th ed.) Sunderland, Massachusetts: Sinauer Associates.

Tam, N.F.Y. & Wong, Y.S. (1995). Mangrove soils as sinks for waste-water-borne pollutants. *Hydrobiologia*, ***295***, 231-241.

Terrados, J., Thampanya, U., Srichai, N., Kheowvongsri, P., Geertz-Hansen, O., Boromthanarath, S., Panapitukkul, N. & Duarte, C.M. (1997). The effect of increased sediment accretion on the survival and growth of Rhizophora apiculata seedlings. *Estuarine Coastal and Shelf Science*, ***45***, 697-701.

Thampanya, U., Vermaat, J.E. & Duarte, C.M. (2002). Colonization success of common Thai mangrove species as a function of shelter from water movement. *Marine Ecology-Progress Series*, ***237***, 111-120.

Thom, B.G. (1967). Mangrove ecology and deltaic geomorphology - tabasco Mexico. *Journal of Ecology*, ***55***, 301.

Thom, B.G. (1984). *Coastal landforms and geomorphic processes*. th ed.) Paris: UNESCO.

Tomlinson, P.B. (1986). *The Botany of Mangroves*. (1th ed.) Cambridge, UK: Cambridge University Press.

Tomlinson, P.B. & Cox, P.A. (2000). Systematic and functional anatomy of seedlings in mangrove Rhizophoraceae: vivipary explained? *Botanical Journal of the Linnean Society*, ***134***, 215-231.

Tri, N.H., Adger, W.N. & Kelly, P.M. (1998). Natural resource management in mitigating climate impacts: the example of mangrove restoration in Vietnam. *Global Environmental Change-Human and Policy Dimensions*, ***8***, 49-61.

Vaiphasa, C., De Boer, W.F., Panitchart, S., Vaiphasa, T., Bamrongrugsa, N. & Santitamnont, P. (2007). Impact of solid shrimp pond waste materials on mangrove growth and mortality: a case study from Pak Phanang, Thailand. *Hydrobiologia*, ***591***, 47-57.

van Mensvoort, T. (1998). Mangrove Research Discussion List Communication.

Verheyden, A., Kairo, J.G., Beeckman, H. & Koedam, N. (2004). Growth rings, growth ring formation and age determination in the mangrove Rhizophora mucronata. *Annals of Botany*, ***94***, 59-66.

Verheyden, A., Roggeman, M., Bouillon, S., Elskens, M., Beeckman, H. & Koedam, N. (2005). Comparison between delta C-13 of alpha-cellulose and bulk wood in the mangrove tree Rhizophora mucronata: Implications for dendrochemistry. *Chemical Geology*, ***219***, 275-282.

Villagra, P.E. & Junent, F.A.R. (1997). Wood structure of Prosopis alpataco and P-argentina growing under different edaphic conditions. *Iawa Journal*, ***18***, 37-51.

Villar-Salvador, P., Castro-Diez, P., Perez-Rontome, C. & Montserrat-Marti, G. (1997). Stem xylem features in three Quercus (Fagaceae) species along a climatic gradient in NE Spain. *Trees-Structure and Function*, ***12***, 90-96.

Waisel, Y. (1972). *Biology of Halophytes*. th ed.) New York: Academic Press.

Walsh, G.E., Holliste, T.A. & Forester, J. (1974). Translocation of 4 organochlorine compounds by red mangrove (Rhizophora-mangle L) seedlings. *Bulletin of Environmental Contamination and Toxicology*, ***12***, 129-135.

Wullschleger, S.D., Tschaplinski, T.J. & Norby, R.J. (2002). Plant water relations at elevated CO2 - implications for water-limited environments. *Plant Cell and Environment*, ***25***, 319-331.

Zwieniecki, M.A., Hutyra, L., Thompson, M.V. & Holbrook, N.M. (2000). Dynamic changes in petiole specific conductivity in red maple (Acer rubrum L.), tulip tree (Liriodendron tulipifera L.) and northern fox grape (Vitis labrusca L.). *Plant Cell and Environment*, ***23***, 407-414.