The role of disturbances in mangrove wood formation and forest structure

Effect of large sedimentation events

Thesis submitted in fulfillment of requirements for the degree of

Doctor of philosophy in Bioengineering Science

of the Vrije Universiteit Brussel and Université Libre de Bruxelles

By

Judith Auma OKELLO

June 2016

Promotors

VUB – Promotor: Prof. Dr. Nico KOEDAM
Laboratory of Plant Biology and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel – VUB, Pleinlaan 2, B-1050 Brussel, Belgium.

Local institution – Promotor: Dr. James Gitundu KAIRO
Kenyan Marine and Fisheries Research Institute (KMFRI)
P.O. Box 81651 - 80100 Mombasa, Kenya.

ULB – Promotor : Prof. Dr. Farid DAHDOUH-GUEBAS
Laboratory of Systems Ecology and Resource Management, Département de Biologie des Organismes, Université Libre de Bruxelles – ULB, Campus de la Plaine, Avenue Franklin D. Roosevelt 50 CPI 264/1, B-1050 Bruxelles, Belgium.

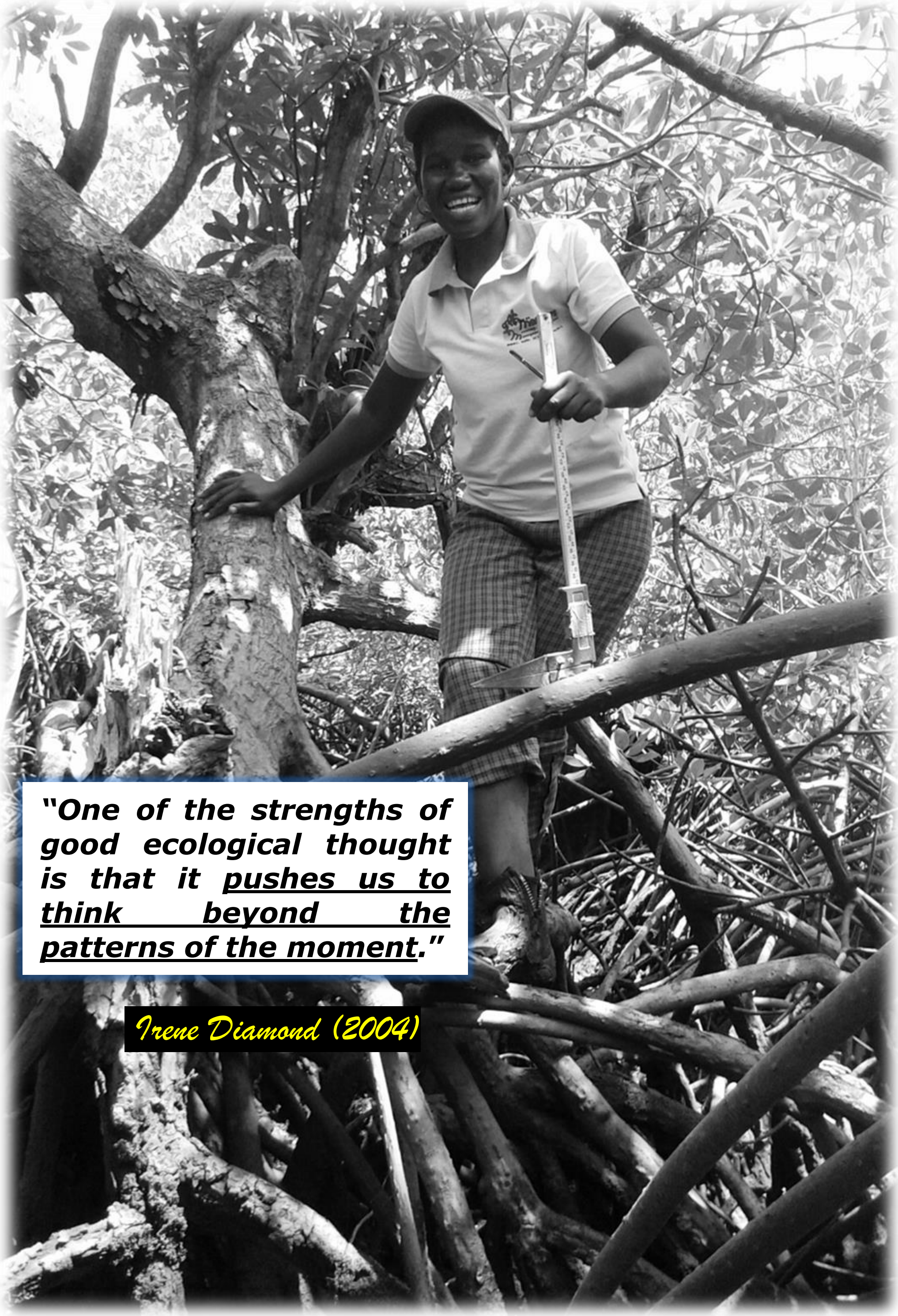
Co-promoter: Dr. Ir. Hans BEECKMAN
Laboratory for Wood Biology and Xylarium, Royal Museum for Central Africa, Leuvense steenweg 13, B-3080 Tervuren, Belgium.

This was a multi-institutional research project involving a collaboration among, the Laboratory of Plant Biology and Nature Management (APNA) of the Vrije Universiteit Brussel (Brussels, Belgium), Kenya Marine and Fisheries Research Institute (Mombasa, Kenya), Laboratory of Systems Ecology and Resource Management of the Université Libre de Bruxelles and the Laboratory of Wood Biology and Xylarium of the Royal Museum for Central Africa (Tervuren, Belgium). It was funded by the Vlaamse Interuniversitaire Raad (VLIR) under the framework of ICP PhD VLIR-UOS programme. Additional funding was provided by the Fonds David et Alice Van Buuren and the Western Indian Ocean Marine Science Association (WIOMSA).

Sponsors

VLIR-UOS and Fonds David et Alice Van Buuren

Contributing institutions



> ***"One of the strengths of good ecological thought is that it pushes us to think beyond the patterns of the moment."***
>
> *Irene Diamond (2004)*

I dedicate this work to my mama Wilfrida Akana Okello who never stepped into a classroom but brought us up to be scholars even after the death of my Father. Mama, though you are now also no more, we began the PhD journey together and you were with me all the way. To my brothers and sisters, daughter Daisy and little son Joe, Together we have made it!!

Acknowledgement

I would wish to acknowledge the support accorded to this study by various individuals and institutions at different levels. To my promoters, prof. Dr. Nico Koedam, Prof. Dr. Farid Dahdouh-Guebas and Dr. James Kairo and co-promoter Dr. Hans Beeckman, for assisting in the design of the project and ensuring overall supervision. Many thanks to Dr. Elisabeth Robert and Dr. Nele Schmitz, for assisting with reading and editing of the write-ups. To the management unit of the Laboratory for Wood Biology and Xylarium, Royal Museum for Central Africa (RMCA), thanks for accommodating me at the institution and granting me access to all the machines, instruments and other materials needed for anatomical work. Thanks to the staff at the Museum that assisted me to get the procedures right within the required time limit. To the forest survey team (Alfred Obinga, George Onduso, Bernard Kivyatu) and the socio economic group (Horace Owiti, Tabitha Muriuki, Edward Waiyaki, George Angwenyi) from KMFRI who helped with data collection in Mtwapa Creek, your invaluable contribution to this work cannot be overlooked. I thank the Kenya Forest Service for providing valuable information on mangrove harvesting and the Mangrove management plan committee for allowing us to use some of the secondary data. I would also like to appreciate the support offered by the entire APNA laboratory members in offering valuable comments that made the write-up much better. To the ANEMA group your consistent support cannot go unmentioned. I feel indebted to my friends Immaculate Odundo, Nancy Oduor and Elisha M’rabu who helped me collect the broken pieces when I lost my data to a thief at the Brussels airport in 2012. Finally, to Vlaamse Interuniversitaire Raad (VLIR-UOS), the Fonds David et Alice Van Buuren and Western Indian Ocean Marine Science Association (WIOMSA), your financial support made my dream turn into a reality.

Table of contents

Summary i

Samenvatting.. v

Résumé... vii

Glossary viii

List of acronyms and magnitudes x

PART I: Introduction and rationale 1

CHAPTER 1: Introduction.. 2

1.1 Mangrove ecology and distribution.. 2

1.2 Mangrove biogeography.. 6

1.3 Mangrove values.. 8

1.4 Threats to mangrove ecosystems.. 10

1.5 The concept of disturbance and alternative stable states.......................... 10

1.6 Sediment dynamics and sedimentation in the mangrove environment 16

1.7 Xylem structure and hydraulic conductance with respect to stress/ disturbance 20

1.8 Mangroves of Kenya 24

CHAPTER 2: The study.. 25

2.1 The species studied: *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*..25

2.2 The study sites 29

2.3 Study rationale... 32

PART II: The mangroves of Mtwapa Creek.. 37

CHAPTER 3: Self-sustenance potential of peri-urban mangroves: a case of Mtwapa Creek Kenya 38

Abstract.. 38

3.1 Introduction 38

3.2 Materials and Methods 40

3.3 Results 46

3.4 Discussion... 54

3.5 Conclusion.. 57

CHAPTER 4: State and future of mangroves of Mtwapa Creek - Kenya as perceived by the local communities 58

Abstract.. 58

4.1 Introduction 59

4.2 Materials and Methods 61
4.3 Results 65
4.4 Discussion...77
4.5 Conclusion 81
PART III: Experimental sedimentation in the mangroves of Gazi Bay, Kenya 83
CHAPTER 5: Effects of experimental sedimentation on the phenological dynamics and leaf traits of replanted mangroves at Gazi Bay, Kenya. 84
Abstract..85
5.1 Introduction 86
5.2 Materials and methods 88
5.3 Results 95
5.4 Discussion...101
5.5 Conclusion 104
CHAPTER 6: Partially buried mangrove trees ensure continued hydraulic conductivity through adjustment in xylem structure. 105
Abstract..105
6.1 Introduction 106
6.2 Materials and methods 108
6.3 Results 113
6.4 Discussion...120
6.5 Conclusions and perspectives 124
CHAPTER 7: Mangrove trees survive partial sediment burial by developing new roots and adapting their root, branch and stem anatomy 126
Abstract..126
7.1 Introduction 127
7.2 Materials and methods 129
7.3 Results 134
7.4 Discussion...144
7.5 Conclusion 146
PART IV: Synthesis...147
CHAPTER 8: General discussion - Conclusions and perspectives...................................148
8.1 Summary of the findings 148
8.2 Disturbance influences forest structure 149
8.3 Resilience of mangroves under instantaneous large sedimentation 150

8.4 Higher or maintained hydraulic conductivity in partially buried mangroves, is it a norm? 153
8.5 Role of nutrients and crab burrowing in partially buried mangroves 154
8.7 Survival of the fittest- mortality among *C. tagal* trees under experimental partial sediment burial 155
8.8 Own perspective 156
8.9 Areas for future research 157
PART V: References and appendices 163
References 164
Appendices: 193
Appendix I: Additional Information 193
Appendix II Mtwapa aerial photograph 197
Appendix IIIa Questionnaires 198
Appendix IIIb Focus group discussion 201

Summary

Mangrove ecosystems constitute a relatively small areal coverage as compared to other tropical forests, yet they are of great benefits to humans as well as an important component of marine biodiversity. These ecosystems are shaped by an interaction of several factors including tides, sediment fluxes, topography and soil and water salinity as well as freshwater input. Secondary influence comes from anthropogenic activities such as exploitation or any other activity that may alter the aforementioned factors. When at a dynamic equilibrium, these factors interact to create a balance and within some level of disturbance, the system in its entirety, the mangroves can still ensure resilience. Extreme forms of disturbances may however disrupt this natural equilibrium resulting in stressful conditions which compromise the resilience capacity of these ecosystems. The ultimate result is degradation of the mangrove wetlands, which in turn not only depletes the resources within their boundaries, but also affects the productivity of adjacent coastal and marine ecosystems.

Sediment deposition and accumulation in mangrove ecosystems play a major role in enhancing substrate stability for better anchorage of the trees, creating new mudflats for further mangrove colonisation and protecting associated ecosystems (sea grass beds and coral reefs) against siltation and eutrophication. However, with increasing demand for agricultural land upstream, the delivery of riverine sediment to the coastal areas is currently increasing with large rivers transporting up to 17.8×10^9 t yr^{-1} (Wilkinson, 2005; Vanacker *et al.*, 2007). Coupled with the Intergovernmental Panel on Climate Change (IPCC) projection of likelihood of heavy rain storms within short durations in the East African region (WWF, 2006; Christensen *et al.*, 2007), the problem may just be accentuated. Sedimentation in mangrove forests results in smothering of the breathing roots of the trees and reduces sediment oxygen. The current study looks at disturbance in mangroves from two perspectives, i) as it occurs in nature and (ii) projected large forms of disturbance as a result of increased anthropogenic pressure and predicted climate change related events with a focus on sedimentation. This information will be important in designing management plans and in deciding management options under climate change scenarios.

Part I of this thesis gives a general introduction and rationale of the study split in two chapters (**Chapter 1 and 2**).

Part II describes the findings of an evaluation of the self-sustenance potential of peri-urban mangroves from an exploitation perspective with a focus on Mtwapa Creek in Kenya. We determined forest structural characteristics (**Chapter 3**) followed by a socioeconomic evaluation of the local human community living in the vicinity (**Chapter 4**). Structural data of the forest studied showed this mangrove forest as having rather sufficient natural regeneration but poor tree development hence compromising the forest's self-sustenance potential. Additionally, proximity to human settlement largely contributed to selective harvesting hence influencing the forest structure. The perception of the local community on the forest status varied with gender, wealth status, education level and knowledge on mangroves, bringing out mixed opinions from the survey. Local communities mainly considered the forest in Mtwapa Creek as degraded but there is a sharp division between lack of suitable construction poles as a form of degradation and cover loss particularly based on gender. More than 50% of the population engaged in farming and the agricultural farms were observed close to the creek with some sighted on the steep slopes facing the creek. This suggests potential increased sediment deposition in the tidal flat. Though they admit depending on mangrove wood, the people distance themselves from full responsibility, blaming the government of not supporting their conservation initiatives and laxity in protecting the forest.

In **Part III** of this study, we assessed phenological dynamics (**Chapter 5**); structure and functioning of xylem vessels and stomatal properties (**Chapter 6)**; and root and bark development (**Chapter 7**) of mangrove trees following experimental instantaneous partial burial. Three mangrove tree species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*) which constitute more than 70% of the mangrove forest formation in the Western Indian Ocean region, were subjected to experimental sediment burial simulating different levels of sedimentation (15, 30 and 45 cm).

Phenological traits of the partially buried trees were monitored over a period of one year **(Chapter 5)**. Leaf loss was found to increase with sedimentation level only in *C. tagal* during the first quarter of the experiment suggesting acclimatisation to the new conditions. There was no significant shift in timing in the phenological events and the leaves produced were of relatively larger surface area in the buried trees of all species as compared to controls. Other observations such as improved fecundity and increased shoot growth as a result of sedimentation were more specific to the different tree species.

In **Chapter 6**, hydraulic conductivity, xylem vessel characteristics of branches and stomata properties of leaves from the partially buried trees were assessed after 14 months of exposure to sedimentation. The results showed an increased hydraulic conductivity capacity in the partially buried trees with up to 3 fold in *C. tagal*. There was, however, a threshold of 15 - 30 cm in some cases above which conductivity had decreased. Based on the observed alteration in vessel diameter, grouping and density following sedimentation (some of which enhanced hydraulic conductivity), the results do not entirely rule out possibility of reduced water uptake imposed by sedimentation but rather suggest a combination of acclimatisation and adaptation of the trees to the exposure.

In **Chapter 7** I attempt to explain the increased hydraulic conductivity and phenological success in the partially buried trees based on adaptation of morpho-anatomical traits of roots and bark in silted trees. The results showed an induction of the phellogen to produce more outer tissue in the buried section of stems in all the three studied species (2 fold increase in *A. marina* and *C. tagal* and 4 fold in *R. mucronata*) following subjection of the trees to increased levels of sedimentation (15, 30 and 45 cm). Root density increased over time with increased levels while the controls maintained a stable number of roots with the new roots assuming anatomical features similar to the original roots.

The study generally established that disturbances (including selective harvesting) may indeed create a structural imbalance in a mangrove forest. However, increased sedimentation in mangrove areas as an outcome of anthropogenic disturbances coupled with climate change impacts may not pose an immediate threat to the mangroves of Mtwapa Creek. Further, my results from the sedimentation experiment affirmed that mangrove tree species like other plants exhibit plastic growth and that sedimentation induces cambial activity hence ability of trees to adapt to resulting changes in environmental conditions. Mangroves are however not solely affected by sedimentation, but face a variety of impacts compounded by human activities. I therefore do not intend to extrapolate these results yet to fit into natural and expected major anthropogenic flooding and sedimentation events that mangroves can withstand in general. Nevertheless, this study provides a good fact-based argument on mangroves’ resilience to sedimentation at least under the conditions in the experimental setup.

Samenvatting

In vergelijking met andere tropische bossen, is de totale oppervlakte van mangrovebossen relatief klein, toch bieden ze veel aan de mensheid en zijn ze van groot belang voor de mariene biodiversiteit. Mangrove-ecosystemen worden gevormd door de interactie van verschillende omgevingsfactoren zoals getijden, zoetwaterinput, sedimentfluxen, topografie en bodemwatersaliniteit, alsook door antropogene activiteiten zoals exploitatie die de omgevingsfactoren kunnen beïnvloeden. Wanneer het dynamisch systeem in evenwicht is, interageren deze factoren om een balans te creëren, en bij minimale verstoringen kan het systeem nog steeds zijn veerkracht behouden. Echter, bij extreme vormen van verstoring kan ook dit natuurlijk evenwicht verstoord worden en stressvolle omstandigheden veroorzaken waardoor het ecosysteem aan veerkracht verliest. Het uiteindelijke resultaat is de degradatie van het mangrove-ecosysteem, waardoor niet enkel de bronnen binnen de grenzen van het mangrovebos worden uitgeput, maar ook de productiviteit van aangrenzende kust- en mariene ecosystemen wordt beïnvloed.

In het eerste deel van deze studie evalueren we het potentieel voor zelfbehoud van periurbane mangrovebossen met een focus op de Mtwapa-kreek in Kenia. We voerden een verkennend onderzoek uit, gevolgd door een socio-economische evaluatie van de lokale menselijke gemeenschap gevestigd in de nabijheid van het mangrovebos. De resultaten toonden een relatief hoge natuurlijke regeneratie van het mangrovebos, maar een lage boomontwikkeling. De nabijheid van de menselijke gemeenschap droeg bij tot selectieve houtkap, waardoor de integriteit van het bos werd gecompromitteerd. Meer dan 50 % van de menselijke populatie zijn betrokken bij landbouw, en hun akkers bevonden zich dichtbij de kreek en in sommige gevallen op de steile hellingen gericht naar de kreek, wat een potentieel verhoogde sedimentafzetting op het intergetijdengebied suggereert. De lokale gemeenschappen waarderen het mangrovebos als een bron van hout voor constructie en brandstof. Toch geloven zij ook dat het bos in een slechte toestand verkeert, die kan verslechteren of verbeteren naargelang de aard van de acties die ondernomen worden, dit in termen van het voorzien van alternatieven en behoud, inclusief een gunstige wetgeving en verbetering van participatief bosbeleid. Hoewel de gemeenschap hun afhankelijkheid van mangrovehout toegeeft, distantieert ze zich van de volledige verantwoordelijkheid en wordt de regering eerder verantwoordelijk geacht voor het gebrek aan ondersteuning van haar initiatieven met betrekking tot bosbehoud en nalatigheid betreffende bosbescherming.

In het tweede deel onderzoeken we het effect van gedeeltelijke “begraving”, bedekking door sedimenten (sedimentatie), op drie mangrovesoorten, *Avicennia marina*, *Ceriops tagal* en *Rhizophora mucronata*, door experimentele sedimentatie in drie niveau’s: 15, 30 en 45 cm t.o.v. het oorspronkelijke grondniveau. We beoordeelden fenologische dynamiek; hydraulische geleidbaarheid; xyleemstructuur en stomatale eigenschappen; en wortel- en schorseigenschappen na “begraving”. De resultaten toonden geen significante verschuiving in de timing van fenologische gebeurtenissen, en het oppervlak van de geproduceerde bladen was relatief groot voor bomen met sedimentatie (in alle soorten) ten opzichte van de controles. De hydraulische geleidbaarheid verhoogde bij de sedimentatieniveaus 15 en 30 cm, en verschilde niet significant verschillend van de controles op 45 cm sedimentatie. Het resultaat van dit sedimentatie-experiment bevestigde hoofdzakelijk dat mangrovesoorten, zoals andere plantensoorten, plastische groei vertonen en dat sedimentatie cambiale activiteit induceert waardoor bomen in staat zijn zich aan te passen aan veranderingen van omgevingsomstandigheden ten gevolge van sedimentatie. Mangrovebossen worden echter niet alleen door sedimentbedekking bedreigd, maar ondergaan verscheidene en gecombineerde impacten door menselijk toedoen. Het is daarom dat ik de resultaten van dit onderzoek nog niet wens te extrapoleren naar alle natuurlijke en verder te verwachten grote antropogene overstromingen en sedimentaanvoer, die de mangrovebossen in algemene zin zouden moeten doorstaan. Niettemin heeft deze studie feitelijk aangetoond dat een zekere veerkracht in de mangrovesoorten aanwezig is, althans tegenover de bestudeerde impacten.

Résumé

Les mangroves couvrent une relativement faible superficie, en comparaison à l'autre forêt tropicale, cependant elles apportent de nombreux bénéfices aux humains tout en étant un composant important de la biodiversité marine. Ces écosystèmes sont régulés par l'interaction de nombreux facteurs comme les marées, l'apport en eau douce, la sédimentation, la topographie, la salinité du sol et de l'eau ainsi que par la pression d'origine anthropique comme l'exploitation ou toute activité modifiant les facteurs cités précédemment. A l'équilibre, ces facteurs interagissent en maintenant cet équilibre et avec peu de perturbations, le système est capable de résilience. Les perturbations extrêmes peuvent cependant interrompre l'équilibre naturel conduisant alors à des conditions stressantes compromettant la capacité de résilience de ces écosystèmes. La conséquence finale est la dégradation des mangroves, ce qui non seulement diminue leurs ressources, mais affecte aussi la productivité des écosystèmes côtiers et marins à proximité.

Dans la première partie de cette étude, nous avons évalué le potentiel de croissance durable d'une mangrove péri-urbaine dans le cas de l'estuaire de Mtwapa au Kenya. Nous avons conduit une étude de la structure suivie d'une évaluation socio-économique de la communauté vivant dans les environs. Les résultats indiquent que la mangrove présente une forte régénération naturelle mais un faible développement de ses arbres. De plus, la proximité des habitations a grandement contribué à la récolte sélective, compromettant donc l'intégrité de la forêt. Plus de 50% de la population participait aux travaux agricoles et les fermes étaient observés à proximité de l'estuaire où certaines étaient installées sur les pentes raides faisant face à l'estuaire, suggérant une sédimentation plus importante sur la zone d'inondation.

Dans une seconde partie, nous avons étudié l'effet d'un enterrement partiel de trois espèces de mangroves, *Avicennia marina*, *Ceriops tagal* et *Rhizophora mucronata*, à travers l'expérimentation de trois niveaux de sédimentation à 15, 30 et 45 cm. Nous avons évalué les dynamiques phénologiques, la conductivité hydraulique, la structure du xylème et les propriétés des stomates, ainsi que le développement des racines et de l'écorce après le recouvrement. Les résultats ne montrent pas de changement significatif dans le déroulement des événements phénologiques et la surface foliaire des feuilles produites était relativement grande chez toutes les espèces recouvertes. La conductivité hydraulique a augmenté pour un faible niveau de sédimentation et n'était pas significativement différente des contrôles pour un recouvrement de 45 cm. Les résultats de cette expérience suggèrent que les espèces de mangroves, tout comme d'autres plantes, sont capables de réguler leur développement et que la sédimentation provoque à l'activité du cambium démontrant alors la capacité des arbres à s'adapter à la fluctuation des conditions environnementales. Les mangroves ne sont pas

cependant affectées par le sédimentation mais font face à des divers impacts liés aux activités humaines. Dès lors, je n'ai pas l'intention d'extrapoler ces résultats pour déterminer l'intensité des perturbations potentielles auxquelles les mangroves pourraient faire face, qu'il s'agisse d'inondation ou de sédimentation d'origine naturelle ou anthropique. Néanmoins, cette étude fournit d'amples arguments qui soutiennent la résilience des mangroves.

Glossary

The glossary below also lists terms and concepts which are widely used in the literature, but are defined here in the context of my work, i.e. in a particular or restricted meaning.

Acclimatization: - the response of an organism or an entire system physiologically or behaviourally to changes in its environment (without developing unique features), allowing it to maintain performance.

Accretion: - a process by which particulate matter are trapped or accumulated by a system. In the case of mangroves, the process is facilitated by the aerial roots**.**

Adaptation: - a phase in reaction by plants (in this case mangrove trees) towards a stress/ disturbance factor involving permanent changes in the organism resulting in its fitness and survival. This may be at evolutionary level (giving rise to diversity) or at ecological level which I refer to in this study.

Cavitation: - the entry and subsequent expansion of air within a plant's water column (in this case the xylem vessels) that can lead to an air-vapor embolism (Hacke, 2015).

Cryptic ecological degradation: (in case of mangroves) - the loss of ecological functionality of mangroves as an ecosystem without change in its spatial extent.

Disturbance: - activities or processes which cause a temporary or permanent shift in environmental characteristics towards less or more favourable conditions.

Embolism: - the sudden blockage of a vessel by an embolus (any material, but also air bubble), preventing transport through the affected vessel.

Erosion: - the gradual process or action of removal of layers of something from a location by an agent. In the case of sediment, the agents may include wind, water or ice as well as abiotic processes leading to wearing out of the earth surface.

Hydraulic safety margin: - a measure of cavitation resistance obtained by subtracting the xylem water potential causing 50% loss of conductivity (Ψ_{50}) from the stem water potential ($\Psi_{stem/min}$).

Natural sedimentation rates: - rates that occur under natural conditions without anthropogenic influences. It is presumed that such rates allow accretion in the mangroves while maintaining breathing roots above the ground level for aeration.

Resilience: - the capacity of a system to absorb an impact and later on return to its original status either after withdrawal or with the causative agent still prevailing

Sedimentation: - the act or process of deposition, or settling as sediment

Sediment burial: - the rapid addition of sediment into an ecosystem thus resulting into either partial or complete coverage of organisms (flora and fauna). This may be instantaneous or it can be a gradual process.

Self-sustenance potential: - the ability of a system to maintain provision of associated goods and ecological roles in the present without compromising its future potential with no or minimal human assistance

Siltation: - the act or process of deposition but only specific to fine particle size sediment**.**

Stress: - a condition which negatively influences growth and development of trees (in this case, mangroves) thus preventing formation of biomass. This may not be immediately lethal conditions and can occur either permanently or sporadically in a locality.

Structural survey: - is the assessment of forest conditions focusing on regeneration and mature tree growth parameters in a given area

List of acronyms and magnitudes

A_{vessel}: Vessel lumen area

$A_{conductive}$: Potential conductive area

CFAs: Community Forest Associations

De: Equivalent vessel diameter

IPCC: Intergovernmental Panel on Climate Change

KFS: Kenya Forest Services

K_h: Native branch hydraulic conductivity

K_L: Hydraulic conductivity standardised for leaf area

K_S: Hydraulic conductivity standardised for xylem area

P_{50}: The xylem pressure at which 50% of the vessels loose their conductive availability

ppt: The units for measuring concentrations in this case salinity (parts per thousand)

VGI: Vessel grouping index

Ψ: Pressure applied in pushing fluid through a branch segment during measurement of hydraulic conductivity

PART I

Introduction and Study Rationale

CHAPTER 1: Introduction

1.1 Mangrove ecology and distribution

1.1.1 The mangrove environment

The definition of the term mangrove has been evolving over time (Macnae, 1968; Tomlinson, 1994; Spalding *et al.*, 1997). The most recent definition was coined by Mukherjee *et al.* (2014) using a Delphi survey conducted between 2011 and 2012. In this survey, involving mangrove experts round the globe, coming to a consensus through an anonymous reviewing procedure, mangroves were referred to as woody plants that normally grow in tropical and subtropical latitudes along the land-sea interface, bays, estuaries, lagoons, and backwaters and as the forest community that these plants and their associated organisms constitute, also called ‘mangal’. The mangal and its associated abiotic factors then constitute the mangrove ecosystem (Mukherjee *et al.*, 2014). The mangrove ecosystem can be classified based on structural and functional features as well as geophysical processes and landscape position. The categories thus include overwash, islands, riverine, basin, fringe, hammock and scrub forests (Lugo and Snedaker, 1974).

According to Tomlinson (1994), mangrove plant species can be broadly grouped into three categories: major elements, minor elements and mangrove associates. Whereas the major elements (major species) possess all or most of the features listed below but always the first two, the minor components (minor species) do not fulfil the second criterion and may lack or have not well developed either.

(i) They grow only in the intertidal flat and do not extend into terrestrial communities.
(ii) They play a major role in the structure of the community and are able to form pure stands.
(iii) They possess morphological specialisation including aerial roots and vivipary.
(iv) They have a physiological mechanism for salt exclusion and/or salt excretion.
(v) They are taxonomically isolated from their terrestrial relatives.

Both the major and minor species are termed true mangroves and there are 70 species according to a review by Polidoro *et al.* (2010). Alemán *et al.* (2010; Table S1) defined a total of 77 species representing 14 families, though any categorisation at some level can generate debatable boundaries. The mangrove associates on the other hand are not restricted to the mangrove environment as they are also found in the adjacent terrestrial habitat (Lacerda *et al.*, 2002; Wang *et al.*, 2010; Mukherjee *et al.*, 2014). The mangrove associates are grouped into four families consisting of 11 species (Table S1). The associates also differ considerably from the true mangroves in their leaf traits and osmotic properties including concentration of various elements in the leaves (Wang *et al.*, 2011), and may not have the same functionality as the true mangroves (Dahdouh-Guebas *et al.*, 2005a; Koedam and Dahdouh-Guebas, 2009; Wang *et al.*, 2010).

1.1.2 Adaptation of mangrove trees to their environment

The mangrove environment is quite variable, characterised by periodic fluctuations with brackish or saltwater and extremes in physicochemical parameters such as salinity (Archibold, 1995). In addition, the habitat is unstable due to exposure to wave action and is mostly waterlogged hence the soils are also oxygen-deficient. In certain areas, mangrove soils may become extremely hypoxic (and even anoxic) as a result of virtual exclusion of free oxygen due to long periods of water logging giving rise to a characteristic pungent smell due to sulphate reduction. The level of hypoxia varies with distance from the sea (Matthijs *et al.*, 1999), sediment depth and levels of organic carbon (Marchand *et al.*, 2011) as well as species composition (Marchand *et al.*, 2004).

Despite being facultative halophytes (Wang *et al.*, 2010) and not possessing qualities of complete hydrophytes, mangroves have successfully colonized the intertidal flats facilitated by the morphological specializations, physiological mechanisms as well as reproductive adaptations among the tree species (Hutchings and Saenger, 1987; Saenger, 2002). These adaptations have been suggested to create an enabling environment for mangroves to escape competition from other offshore marine biotopes and be able to persist in the intertidal zone where vines as well as other trees and shrubs cannot (Janzen, 1985). In addition mangroves are disturbance and stress tolerant both at species and ecosystem level (Hutchings and Saenger, 1987).

Strong waves and hypoxic conditions – Mangrove trees have well developed root networks. This is the most conspicuous morphological adaptation characteristic of these trees. These roots vary in architecture among species and perform both anchorage and aeration functions (Figure 1.1). The elaborate rooting systems in mangrove species firmly anchor the trees even in unstable mud thus protecting them against the high energy coastal waters (Wolanski *et al.*, 1992). However, due to the hypoxic substrata, most mangrove tree species have shallow cable root system with aerial breathing roots and numerous extensive lateral roots for support. The aerial roots are covered by numerous lenticels which are simply loose aggregates of air filled cells (air lacunae) that facilitate in the breathing process (Tomlinson, 1994). Whereas oxygen can passively diffuse through the lenticels (in less inundated sites) thus facilitating direct gaseous exchange between atmosphere and sediment (Tomlinson, 1994), the well-developed system of air lacunae in the roots allows transport of CO_2 from the root lacunae to the leaves and O_2 from the leaf lacunae to the roots (Wong, 2004). In areas where the roots are frequently covered through tidal inundation, atmospheric gaseous exchange is achieved through pressure imbalance created by their alternating immersion and exposure during the tidal cycle (Tomlinson, 1994). Aerial roots and particularly pneumatophores (Figure 1.1) are therefore mainly well developed as a result of the hypoxic conditions in the mangrove environment and as such some mangrove trees growing in well aerated sediment conditions may lack them (Tomlinson, 1994; Dahdouh-Guebas *et al.*, 2007). Conversely, under extreme hypoxic conditions and in more frequently inundated areas the pneumatophores may grow much longer and more numerous to increase surface area for gaseous exchange (Saifullah and Elahi, 1992; Dahdouh-Guebas *et al.*, 2004a; Dahdouh-Guebas *et al.*, 2007). For instance, *A. marina* roots grow up to a height of 20 cm under normal growing conditions. *R. mucronata* from Gazi Bay were found to develop prop roots from up to height of 108 cm to minimum 4 cm on the main stem (Elisabeth M.R. Robert unpublished data).

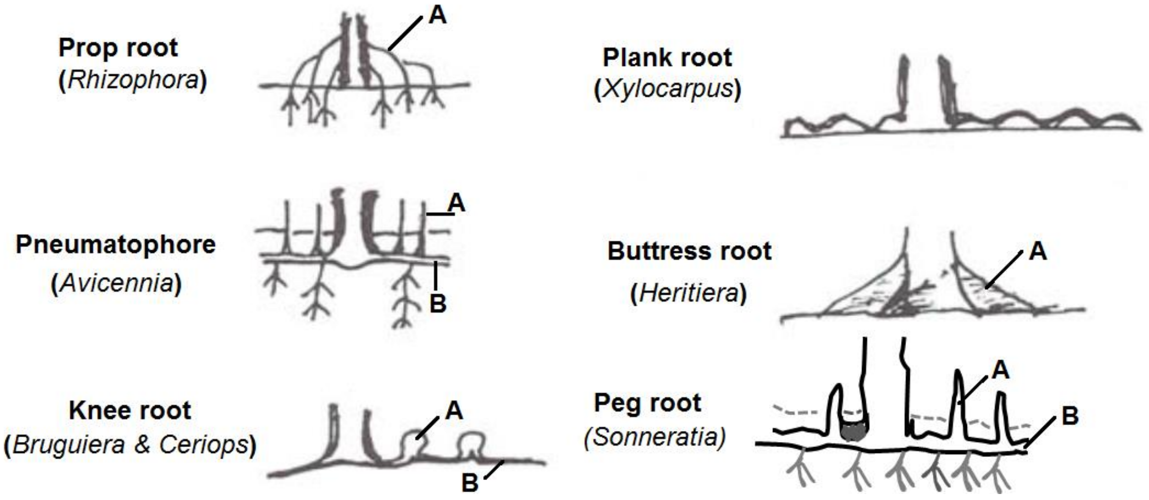


Figure 1.1 Diagrammatic representations of the major forms of aerial root in mangrove trees with the associated species in parenthesis. The aerial and cable components of the roots are marked A and B respectively where applicable. Adapted from Stafford-Deitsch (1996) and Kathiresan and Bingham (2001).

Salinity – As any other plant would, mangrove trees require a given concentration of ions in their tissue to create the correct osmotic potential for efficient absorption of water from the roots and conduction to the leaves (Ball, 1988; Krauss *et al.*, 2008). However, with the relatively high salinity levels of sea water (average 35 ppt); plants growing in the marine environment are adapted to regulate the amount of salts in their tissue. In mangroves, various salt regulation mechanisms have evolved; including exclusion, extrusion or accumulation. Additionally, different mangrove tree species have various ranges of salinity within which they can cope. Salt exclusion occurs during water uptake at the roots with the aid of ultra-filters while salt extrusion is through salt glands in leaves or cork warts. Salt exclusion may however result in increased accumulation around the rhizosphere resulting in high osmotic potentials. This is counteracted by the gelatinous, polymeric substances in the sap that limit water flow rate and lower transpiration rates (Zimmermann *et al.*, 1994). The salt storing species keep the excess salt deposits locked away in older senescing leaves (Tomlinson, 1986; Werner and Stelzer, 1990). Mangroves may also ensure water use efficiency through production of succulent leaves with a thick cuticle to conserve desalinated water and nutrients (Longstreth and Nobel, 1979; Borkar *et al.*, 2009; Scott *et al.*, 2014). Other studies have also shown wood anatomical adaptation of mangrove trees to high salinity. Such adaptations have been noted in increased vessel grouping and vessel densities of *Avicennia marina* and *Rhizophora mucronata* (Schmitz *et al.*, 2006; Robert *et al.*, 2009a).

Reproduction – Mangrove tree species reproduce sexually by means of flowers that are in most cases relatively small in size and are commonly pollinated by both wind and insect (Coupland *et al*., 2006). Through vivipary, some mangrove tree species enhance the survival of their young individuals by ensuring continuous growth of the offspring (propagules) while still attached to the mother plant before they are released into the environment (Tomlinson, 1986). During the period when the propagule is still attached, the young plant is given an opportunity to develop some tolerance and accumulate sufficient nutrients to assist quick rooting in the substratum after release (Bhosale and Mulik, 1991 cited in Kathiresan, 2001; Smith and Snedaker, 1995). The propagule is buoyant easing dispersal through floating over long distances while the shape increases the chances of self-planting whenever it drops to the substrate. The non-viviparous mangrove species on the other hand produce large fruits which can easily float (Kathiresan and Bingham, 2001). In addition, mangrove trees either produce many propagules which enhance survival or fewer but larger propagules that anchor faster and are less prone to predation by crabs (De Ryck *et al.*, 2012). Depending on the density of the propagules and the angle at which they float, wind also plays a quite significant role in dispersal trajectories of the propagules (Van der Stocken *et al.*, 2013).

1.2 Mangrove biogeography

Globally, mangroves can be divided into Atlantic East Pacific (AEP) and Indo-West Pacific (IWP). The AEP mangroves constitute those found in West America, East America and West Africa while the IWP are those in East Africa, Indo-Malesia and Australasia (Alongi, 2009; Figure 1.2). The most diverse mangrove region is found in the IWP with the most species rich being the Indo-Malay Philippine Archipelago (Alongi, 2009; Polidoro *et al*., 2010). The latest and most comprehensive mapping of mangrove forests put the areal coverage of these forests at an estimated value of 13,776,000 ha distributed over the shores of 118 countries (Figure 2a; Giri *et al.*, 2011).

Mangrove forests generally grow in the tropical and subtropical climate, reaching their maximum development and greatest luxuriance where rainfall is high and not seasonal while occurring as shrubs in desert areas (Macnae, 1968). The former include parts of South East Asia, Malaya, Sumatra and parts of Borneo while the latter occur in areas such as the Arabian peninsula (Saudi Arabia; Macnae, 1968) and the northernmost mangroves of West Africa (Dahdouh-Guebas and Koedam, 2001). The global distribution of the mangrove ecosystem is however restricted to the intertidal shores of the tropics and subtropical region between 30° North and South of the equator (Tomlinson, 1994; Kathiresan and Bingham, 2001; Giri *et al.*, 2011; Quisthoudt *et al.*, 2013). These latitudinal limits of mangrove distribution are governed by major ocean currents and the 20°C isotherm of seawater during the yearly coldest month (Alongi, 2002). Possible changes in the limits have, however, been predicted indicating further South extension for *A. marina* and *B. gymnorrhiza* (Quisthoudt *et al.*, 2013). The latitudinal limit extension is largely related to the amount of heat limiting growth rather than extreme temperatures (Quisthoudt *et al.*, 2013).

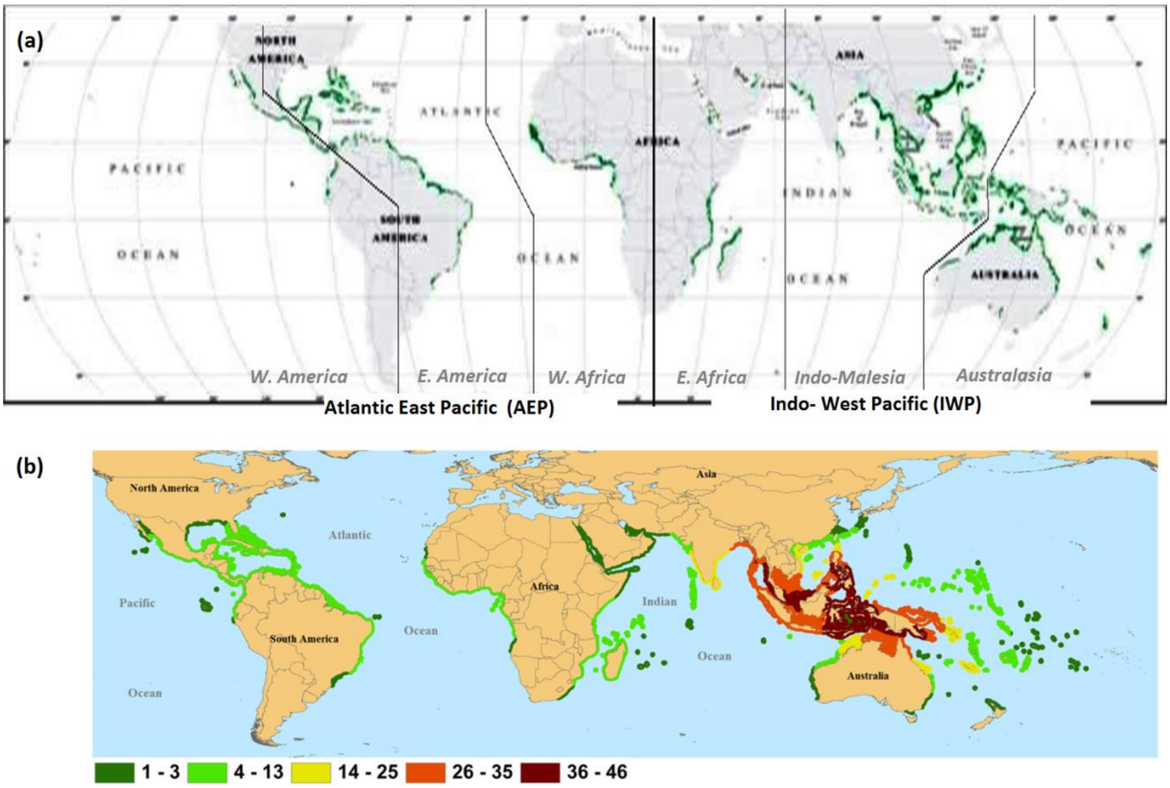


Figure 1.2 a) World mangrove distribution adopted from Giri *et al*. (2011) and Alongi (2009); **b)** mangrove species richness excluding the introduced ranges of *Rhizophora stylosa* in French Polynesia, *Bruguiera sexangula*, *Conocarpus erectus*, and *Rhizophora mangle* in Hawaii, *Sonneratia apetala* in China, and *Nypa fruticans* in Cameroon and Nigeria (Polidoro *et al.*, 2010).

On a regional scale, extensive development of mangrove forests mainly occurs in the estuaries of large rivers flowing over shallow continental shelves. Factors such as salinity, tidal fluctuation, sediment characteristics and wave energy are considered as the major determinants for spatial distribution of mangroves (Tomlinson, 1986; Ball, 1988). In any given area where mangroves occur, the tree species are limited in number unlike in tropical forests. Mangrove forests are made up mainly of monospecific stands or mixtures of not more than three species (Krauss *et al.*, 2008) with an understory often covered with seedlings and saplings of the overstory (Ball, 1980; Snedaker and Lahmann, 1988). The different tree species occur in varying abundance and frequency within the tidal flats giving rise to zones. Zonation in mangroves often results in monospecific bands of vegetation growing parallel to the shoreline, tidal channels and estuaries. This may however vary from one geographic region to the other due to differences in floristic composition of mangrove communities (Feller and Stink, 1996). In addition there may be considerable overlap of bands of species in their range of tolerance considering eco-physiological hypothesis of zonation (Ball, 1988). Zonation is thus not always evident in most mangroves as it may vary considerably with local conditions such as salinity and soil pH (Satoru *et al.*, 1994) and could also be disrupted by anthropogenic disturbances (Polidoro *et al.*, 2010). In general, scientific explanations into why zonation in mangroves revolves around five schools of thought: Plant succession, geomorphology, physiology, ecology and population dynamics (Snedaker, 1982).

1.3 Mangrove values

Mangrove ecosystems are important for the wide range of goods and services which the local human communities and tropical economies benefit from. These include wood and wood products such as timber, fuelwood[▲], tannin, dye, traditional medicine, honey and fodder (Dahdouh-Guebas *et al.*, 2000; Walters *et al.*, 2008). Further, mangroves play a role in the protection of shorelines against erosion and storms and consequently preventing lives and property from destruction (Betagoda, 2003; Dahdouh-Guebas *et al.*, 2005b; Gunawardena and Rowan, 2005; Kathiresan and Rajendran, 2005; Alongi, 2008; Barbier *et al*., 2011). Their position in the ecotone between land and sea may also provide a protective wall for the offshore ecosystems (seagrass beds and coral reefs) preventing them from being silted up and getting nutrient overload (Bouillon *et al.*, 2008; Robertson and Phillips, 1995). These wetlands provide essential ecosystem services: (i) they act as spawning, breeding and nursery grounds for a number of fish species (Nagelkerken *et al.*, 2000; Crona and Rönnbäck, 2005, 2007); (ii) they provide habitat for several vertebrates and invertebrates and (iii) they are feeding grounds for certain marine fish (Huxham *et al.*, 2004). The value of mangroves as nursery grounds has however been noted to be ubiquitous following their insignificant contribution to coral fishes at community level in certain regions (Lee *et al*., 2014).

With the current worldwide concern about climate change effects, mangrove forests have been marked as one of the most effective natural ecosystems that could help curb the threat of global warming due to their high productivity hence capacity to sequester high levels of CO_2 (Meepol, 2010; Cerón-Bretón *et al.*, 2011; Donato *et al.*, 2011; Kridiborworn *et al.*, 2012). In Kenya, the 'Mikoko Pamoja' project which is the first ever running mangrove carbon project has been initiated in Gazi Bay with an aim of maintaining and enhancing carbon stocks (while improving the local communities livelihood) through generating and selling carbon credits to companies and individuals seeking to improve their green credentials through offsetting their carbon footprint.

[▲] fuelwood is any form of wood used as fuel and may refer to both charcoal and firewood.

Mangroves may also act as land builders, at least in one direction through vertical accretion hence increase in soil volume (Lee *et al*., 2014). This would be particularly important for maintaining the mangrove ecosystem following the foreseen rise in sea-level (SLR) at least under the low scenario projected at about 0.3 m by the year 2100 (IPCC, 2014).

Owing to the fact that mangrove goods are limited and that there is difficulty to attach internationally accepted value to their services, these ecosystems are normally undervalued (Ong and Gong, 2013). There are also several ways for valuing ecosystem services and the different methods used in different locations give variant results. As a result, several studies attempting to attach monetary value to mangrove services have come up with large variations for the same service depending on method used and area under consideration (Table 1.1). According to a recent Delphi survey conducted by Mukherjee *et al*. (2014), experts rated import and export of carbon and primary production highest among all the ecological functions of mangroves.

Table 1.1 Value of mangrove ecosystem as reported in various parts of the world by different studies (euros converted on a 3% discounting rate). Compiled from Dahdouh-Guebas, 2013

Function, good or service	**Value (EUR.ha^{-1}.yr^{-1})**	**Country**	**Reference**
Forest products	373-450	TH	Barbier, 2007
Construction wood	278	KE	Kairo *et al.*, 2009*
	2234	KE	Mwakha, 2011
Fuelwood	14	KE	Kairo *et al.*, 2009*
	85-151	KE	Mwakha, 2011
Coastal protection	3625	multiple	Costanza *et al.*, 1989
	2838	TH	Sathirathai & Barbier, 2001
	6,916-8,347	TH	Barbier, 2007
	1,224	KE	Kairo *et al.*, 2009*
	393	KE	Mwakha, 2011
	9,640-11,634	multiple	Barbier *et al.*, 2011
Fisheries	656-12.920	multiple	Rönnbäck, 1999
	546-761	TH	Barbier, 2007
	87	KE	Kairo *et al.*, 2009*
	233	KE	Mwakha, 2011
Education and research	594	KE	Kairo *et al.*, 2009*
	30	KE	Mwakha 2011
Carbon sequestration	34	KE	Kairo *et al.*, 2009*
Carbon sequestration	1,159	KE	Mwakha , 2011
Tourism	7	KE	Kairo *et al.*, 2009*
Phytoremediation	4,489	FJ	Lal, 1990
	920	MX	Cabrera *et al.*, 1998
Biological control	5	KE	Mwakha, 2011
Existence and heritage	84	KE	Mwakha, 2011

Function, good or service	**Value (EUR.ha^{-1}.yr^{-1})**	**Country**	**Reference**
Forest products	373-450	TH	Barbier, 2007
Habitat/refuge	193	KE	Mwakha, 2011
Leisure	74.991	KE	Mwakha, 2011
Nutrient cycling	20.865	KE	Mwakha , 2011
Waste treatment	7416	KE	Mwakha , 2011
Total integrated value	**7,835-9,558**	TH	Barbier, 2007
Total integrated value	7,701	multiple	Costanza *et al.*, 1997
Total integrated value	2,238	KE	Kairo *et al.*, 2009*
Total integrated value	107.688	KE	Mwakha , 2011

1.4 Threats to mangrove ecosystems

Despite the multiple benefits and the growing appreciation of these services over the past decades, mangroves around the world still face significant increasing threats from various sources (FAO, 2007c). Different forms of degradation have been outlined by Mukherjee *et al.* (2014) of which development related degradation was enlisted to have the greatest impact on mangroves and may take the longest time to recover and regain functionality. Mangrove degradation may result from quantitative and/or qualitative loss of this ecosystem (Shah *et al.*, 2007). Quantitative loss results in reduction in aerial coverage while qualitative loss leads to cryptic ecological degradation which in most cases may go unnoticed initially. Quantitative loss of mangrove cover worldwide have been estimated and documented over the years indicating a progressive annual loss of 2% from 1980 (Spalding *et al.*, 1997) to the 13,776,000 ha in the year 2000 (Giri *et al.*, 2011) which is 12% smaller than the FAO (2007c) estimates. Regionally, the Indo-Malay Philippine Archipelago has one of the highest rates of mangrove loss reported, with about 30% reduction between 1980 and 2005 (FAO, 2007c). In Kenya, 18% of the mangrove cover was lost between 1985 and 2010 with the highest loss experienced between 1992 and 2000 (Kirui *et al.*, 2012). However, with the relatively low decline of only 8% estimated from 1985 to 2005 (Spalding *et al.*, 2010), it is in fact possible that most of the loss was from 2005 to 2010.

1.5 The concept of disturbance and alternative stable states

Grime (1979, 2001) defined disturbance as mechanisms which limit the plant biomass by causing its partial or total destruction and stress as the external constraints which limit the rate of dry matter production of all or part of the vegetation. Disturbance may either precede stress or can co-occur. The former includes landslides, flooding, grazing, harvesting, and scorching from the sun while the latter includes drought, hypoxia and anoxia, salinity, metal toxicity.

One of the widely accepted theories in plant ecology that explain differential management of stress and disturbance among species is the Universal Adaptive strategy theory of Philip Grime commonly referred to as Grime's C-S-R triangle (Grime, 1974; 1977; 1979; Hodgson *et al.*, 1999; Grime 2001; Caccianiga *et al.*, 2006). This is in addition to Tilman's resource-ratio hypothesis (Craine, 2005; Tilman 1985) which attempts to explain succesion based on interspecific competition for resources and long term pattern of supply of limiting resources (Tilman, 1985).

According to Grime's theory, variations occuring in the environment impose temporal constraints on resource acquisition. It is based on three basic life-history strategies (competitors-C, stress tolerants-S and ruderals-R) that plants may adopt during establishment and growth. The three strategies are derived from the possible combinations of environmental stress and disturbance levels, to which plants can be adapted. With the combination of both high stress and disturbance not being conducive to plant growth, three life strategies emerge, hence the triangle in which every species can be positioned according to Grime *et al.* (1988). These strategies each of which is found in species occupying a given habitat is characterised by separate sets of ecological, morphological and physiological traits (Figure 1.3). According to C-S-R, in high disturbance habitats there will be no difference in species composition between competition and stress sites and that in stressful habitats competition will be low. The C-S-R model has nevertheless received criticism and support in almost equal measure with its critics arguing that it is based largely on empirical grounds and that it has limited utility as a predictive model in community ecology (Silvertown, *et al.*, 1992; Wilson and Lee, 2000).

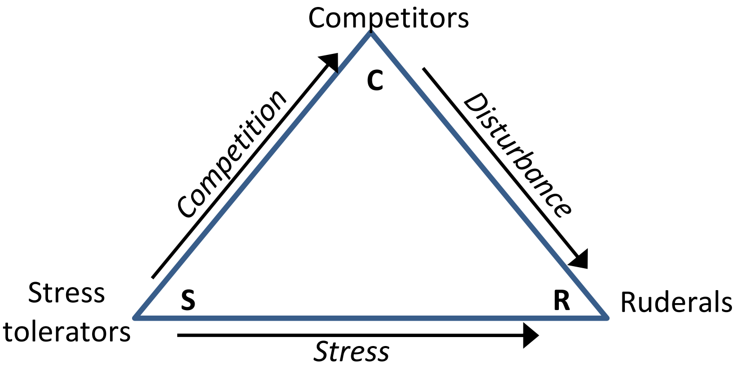


Figure 1.3 Grime's C-S-R triangle (Redrawn from Grime *et al.*, 1988 and Hodgson *et al.*, 1999)

In any ecosystem various elements interact to create a stable state where the organisms can thrive in. Disturbances may alter the processes that take place in such a system thus influencing important demographics such as propagule dispersal, recruitment and survival. While still in a stable state the conditions may remain steady and do not change over time as a change in one direction is counteracted by one in the opposite direction (Figure 1.4). According to Beisner *et al*. (2003), there has to occur an extreme form of disturbance to make the system shift entirely into an alternative stable state. Though at this new domain it is still considered stable, the conditions will be different as to even lead to colonisation by new species and loss of once occurring ones (Scheffer *et al*., 2001). Such switches from one state to the other may be triggered by several events but it is mainly due to loss of resilience (Scheffer *et al*., 2001).

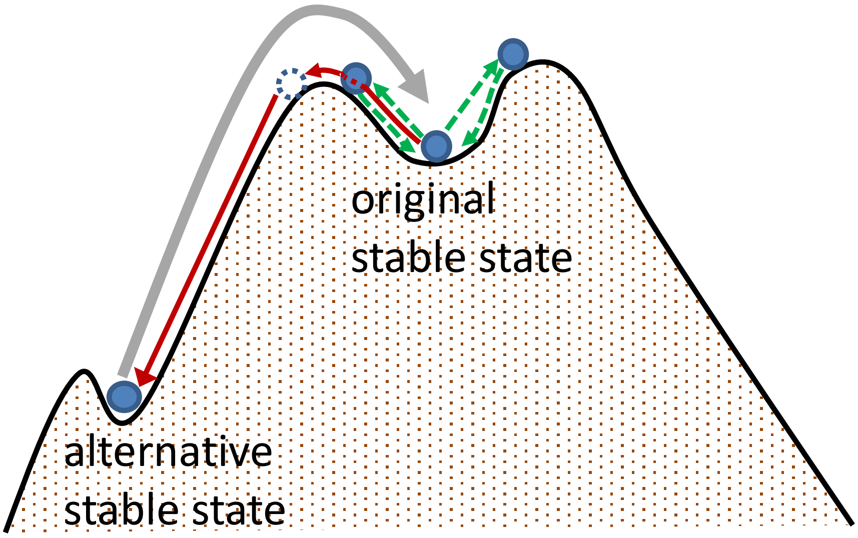


Figure 1.4 Diagram representing effect of disturbance on the state of an ecosystem. The green dotted lines indicate changes that are balanced, the red line is a change that pushes the system into the alternative stable state; the grey thick arrow is the change required to push the system back to its original stable state. Adapted from the ball and cup analogy by Beisner *et al*. (2003) and descriptions by Scheffer *et al*. (2001)

Once the alternative stable state is achieved, it requires greater opposite force to catapult the system back to its original stable state (represented by the grey line in Figure 1.4). This idea that communities can be found in one or several stable states was proposed by Lewontin (1969) and has since gained popularity among other ecologists (Connell and Sousa, 1983; Beisner *et al*., 2003; Didham *et al*., 2005). According to Didham *et al*. (2005), both disturbance and stress are linked to the occurrence of alternative stable states (ASS). Mason *et al.* (2007) later added that with disturbance the link can only be true as long as the ecosystem can return to its pre-perturbation state after the release. This fact reiterating the three major criteria of ASS as set by Connell and Sousa (1983). Mason however, discredits the arguments of Didham *et al*. (2005) on stress, stating that there is very little evidence associating it with ASS particularly in the real stress prone ecosystems.

1.5.1 Role of disturbance in a mangrove ecosystem

Mangrove ecosystems are not only influenced by chemical and physical conditions in their environment but also help create those conditions. Mangrove forests are thus able to create conditions that favour colonisation by other animal and plant communities (Viswanathan, 2011) as well as facilitate return of ecosystem services where they have been lost (Rönnbäck *et al.*, 2007). As a result, disturbances to the system can have cascading long term effects. These disturbances alter the processes within these ecosystems and where they result in deterioration of growth conditions, mangrove trees experience inhibition of seedling establishment (Thampanya *et al.*, 2002), dieback, or even mortality of mature stands hence they may be greatly influencing the forest structure (Lovelock *et al.*, 2011) and consequently a total loss of this ecosystem with impacts on those ecosystems that are linked to functional mangroves. However, since disturbances are an integral component in mangrove forest dynamics, it is not always the case that any disturbance influences mangroves negatively (Hauff *et al.*, 2006). For instance, broken branches by wind and storm allows light to reach the seedlings in the understory which then quickly grow to fill in the gaps (Hauff *et al.*, 2006). Several processes of disturbance are intrinsic to mangrove dynamics and much depends on the natural baseline, the causes, the frequency and the magnitude of disturbance whether they should be considered deleterious.

1.5.2 Nature induced disturbances

Natural induced disturbances are often spontaneous, leading to sudden changes in the physical or chemical conditions of the environment inducing varying degree of stress to the mangrove forests. This form of disturbances may result from natural agents such as hurricanes, frost events, droughts, tropical storms and chronic flooding (Ellison and Farnsworth, 1997; Allen *et al.*, 2010). Though such events may be uncommon, drought for instance has been reported to result in decreased rate of radial growth hence impacting negatively on wood production in mangroves (Allen *et al.*, 2001) while the other agents result in tree mortality in forests in general (Allen *et al.*, 2010). Drought introduces changes in river regimes and as such affect the freshwater supply to the estuaries hence increasing salinity which then might go above the tolerance range of certain species (de Lacerda, 2002). Pests and diseases have also been cited as important agents of disturbance in forests causing dieback and tree mortality in mangroves. The forms of attack range from foliar pests and diseases (Gilbert *et al.*, 2002) to infestation by stem boring caterpillars (Drude de Lacerda, 2002; M'rabu *et al.*, Unpublished data). Where deaths do not occur, pest/disease attack may increase the susceptibility of mangrove trees to further deterioration through other forms of disturbances. Although relative sea level rise is also projected to result in a major further loss of mangrove forests in the long run (Gilman *et al.*, 2008; Tran Thi *et al.*, 2014), the other events such as flash floods, and sudden large sediment input may pose immediate threats to this fragile ecosystem (Kitheka *et al.*, 2003; Bosire *et al.*, 2006; M'rabu, 2009).

1.5.3 Human induced disturbance

Human induced disturbances result from anthropogenic activities both within and outside the mangrove areas. While the disturbances taking place at some distance from the mangrove area may not be easily linked to mangrove deterioration, those within the mangrove area can be tracked down with ease. Human disturbances in the mangroves can be classified into three categories: i) extraction of mangroves for economic purposes, ii) reclaiming land for industrialization, urbanization and development, and iii) pollution such as oil spills (Ellison and Farnsworth, 1996a; Mukherjee *et al.*, 2014). Adding on to the list is the introduction of herbivores in the mangroves for instance the browsing of mangroves by the water feral buffaloes, and other domestic animals such as camels, sheep, goats in Arabia and Indus delta of Pakistan (Hogarth, 2015). These animals feed on *Avicennia* leaves, trample on seedlings and compact soil making it difficult for propagule establishment.

Due to their high calorific content, mangroves have largely been utilised in East Africa both for domestic and commercial purposes (de Lacerda, 2002) as fuelwood (firewood and charcoal), leading to overexploitation of the resource (Abuodha and Kairo, 2001). In addition, selective logging of wood resources to suit market demands particularly in poles of a certain diameter has greatly compromised the quality and structural composition of the remaining forest (Dahdouh-Guebas *et al.*, 2000; Walters, 2005; Mohamed *et al.*, 2009). Mangrove forests areas have also in the past been cleared to create space for aquaculture farms, salt mining and other developments deemed a better land use by the developers (Primavera, 1997; Abuodha and Kairo, 2001; Tong *et al.*, 2004; Thampanya *et al.*, 2006; Ellegaard *et al.*, 2014;

Mukherjee *et al.*, 2014). Such destructions have been shown to lead to significant deposition of sediment in estuaries (Ellegaard *et al.*, 2014). The latest major wave of destruction due to mangrove conversion in Kenya has been with the proposed second port to be established in Lamu. Relatively pristine forests in the Manda Bay area from Mkanda Channel to Dodori Creek are being felled to create space for the development of this port (Plate 1.1a; Gubelman, 2009). Accidental spillage and intentional release of pollutants into the mangrove areas due to lack of proper sewage treatment systems have also led to substantial deterioration and loss of mangroves in Kenya (Plate 1.1b; Government of Kenya, 2009).

Plate 1.1 Disturbances in the mangrove ecosystem; From top left (a) mangrove cleared in 2009 to create space for a proposed port development in Lamu, Kenya (Gubelman, 2009); (b) mangrove death due to an oil spill at Makupa creek in 1988, Kenya (Government of Kenya, 2009); (c) *B. gymnorrhiza* forest at Aoa, American Samoa died from siltation (Ellison, 1998) and (d) a section of mangroves in Njia ya Ndovu- Lamu, Kenya dying after sediment from an artificially created channel was dumped in the area resulting in partial burial.

Human induced disturbances from outside the mangrove area degrade the ecosystem indirectly by altering the physical environment of the adjacent mangrove forests. The ultimate destructive pattern of these disturbances is however similar to those within the forest area (Kovacs, 2000). Examples include the development of offshore bars, construction of upland freshwater diversion projects as well as poor farming practises in the riparian and catchment areas (Kovacs, 2000; Valiela *et al.*, 2001). Irrigational manipulations in the catchment areas may result in changes of the hydrology and salinity regime of mangrove areas as well as nutrient inflow and sedimentation patterns and consequently influencing tree species composition significantly (Jayatissa *et al.*, 2002; Dahdouh-Guebas *et al.*, 2005a). Other than natural river discharge, the amount of particulate matter is greatly influenced by human activities particularly poor farming practises and clearing vegetation on slopes along the riparian zone and catchment areas which accelerate sediment transport and deposition in the mangrove areas (Vanacker *et al.*, 2007). Despite the fact that the mechanisms that explain erosion are independent of anthropogenic impacts, all these human induced disturbances may change the frequency and magnitude of erosion rates (Vanacker *et al*., 2014).

1.6 Sediment dynamics and sedimentation in the mangrove environment

Mangrove forests grow best where deposition and accumulation of fine sediments occur and wave energy is low ensuring propagule establishment and strong anchorage capacity of the roots (Tomlinson, 1994). Tidal flow and the subsequent attenuation of water flow within the forest results in the deposition of fine particles from the overlying water column which is also important for further mangrove establishment. Sedimentation occurs naturally in the mangrove areas through accretion facilitated by the complex aerial roots structures which increase surface area of physical barrier for trapping sediment (Hutchings and Saenger, 1987; Kathiresan, 2003; Kimeli, 2013) and is as such considered an important factor in ecology (Hutchings and Saenger, 1987; Robertson and Alongi, 1992; McKee 2011). Moreover, accretion of mineral sediment together with belowground accumulation of mangrove roots and organic material act as aids towards mangroves adjustment to sea level rise (McKee *et al*., 2007; McKee *et al*., 2011).

Transport of suspended sediment particles in the mangrove environment is controlled by seven processes which may however vary in degree of importance from one locality to the other (Wolanski and Gibbs, 1995; Alongi, 2009; Kimeli, 2013). These processes are: tidal pumping, baroclinic circulation, trapping of small particles in the turbidity maximum zone, flocculation, the mangrove tidal prism, physiochemical reactions, and microbial production of mucus. During high tide, sediment particles are retained in suspension by the turbulent wakes created by the aerial roots and tree stems. Most of the deposition occurs within 30 minutes just before slack high tide and cannot be re-suspended due to the high vegetation density and aerial root networks that inhibits water motion (Furukawa and Wolanski, 1996). The efficiency of sediment retention within the mangroves varies among the zones with the *Avicennia-Rhizophora* interphase showing the highest retention capacity (Kathiresan, 2003). Such natural sedimentation levels are only to a magnitude of 1.5 cm per annum allowing for the mangrove aerial roots to acclimatise and keep pace with the change thus maintaining their aeration role to the organism (Hutchings and Saenger, 1987).

Mangrove ecosystems may therefore play an important role in sediment dynamics, particularly where there is extensive forest cover in relation to water ways (Kimeli, 2013). Damage to the mangroves strongly affect sediment budget and promotes coastal wave erosion and consequently increased sedimentation in the mangrove areas thus causing further damage to the ecosystem (Twilley *et al.*, 1996). This has led to change in tree species composition and other secondary effects related to the destruction of the forest including the disappearance of certain mangrove fauna (Hatton and Couto, 1992; Kathiresan and Bingham, 2001). Further, the extent of mangrove destruction influences both magnitude and direction of sediment transport through the enhancement of erosion in such degraded coastlines (Figure 1.5). This results in a net import of sediment and high accretion rates and consequently partial burial of the trees (Kitheka *et al.*, 2003).

During the wet season, a large amount of sediment is imported into the mangrove forests thus compounding the sedimentation problem (Larcombe and Ridd, 1996; Kitheka *et al.*, 2003; Alongi, 2009). This is a function of distal influences including factors affecting sediment loads in rivers such as topography, soil characteristics and increased flooding due to climate change related events (Figure 1.5). In Kenya coastal areas, soils are for instance predominantly unconsolidated coralline material thus prone to erosion (Government of Kenya, 2015). The two main rivers Athi- Galana/Sabaki and Tana draining into the Indian Ocean are reported to deliver several tonnes of sediments into the coastal areas. The former is smaller in terms of drainage area (70,000 km^2) but discharges up to 13 million tonnes per annum while the latter draining an area of 127,000 km^2 brings in 6.8 million tonnes (Government of Kenya, 2015; Brown *et al.*, 1996). This has been largely attributed to degradation in the catchment areas of River Athi-Galana/ Sabaki which saw an increase of sediment delivered by 260 times from the 80’s. From a continental perspective, Vanmaercke *et al*. (2014) compiled sediment yield for 682 catchment areas in Africa revealing large spatial variability which can be explained by various environmental factors. These include differences in topography, vegetation cover and annual runoff depth.

Additionally, mangroves may suffer excessive sedimentation through waste discharge from shrimp ponds as well as from natural sources such as change in beach formation dynamics as has been witnessed in Gazi Bay, Kenya where it has resulted in mortality of a large section of *S. alba* stand (Plate 1d). Further, anthropogenic activities involving clearing of vegetation (Aksornkoae, 1993) and inappropriate farming on slopes bordering the mangrove as observed by Mohamed (2008) in Tudor Creek for instance, may contribute significantly to large sedimentation events.

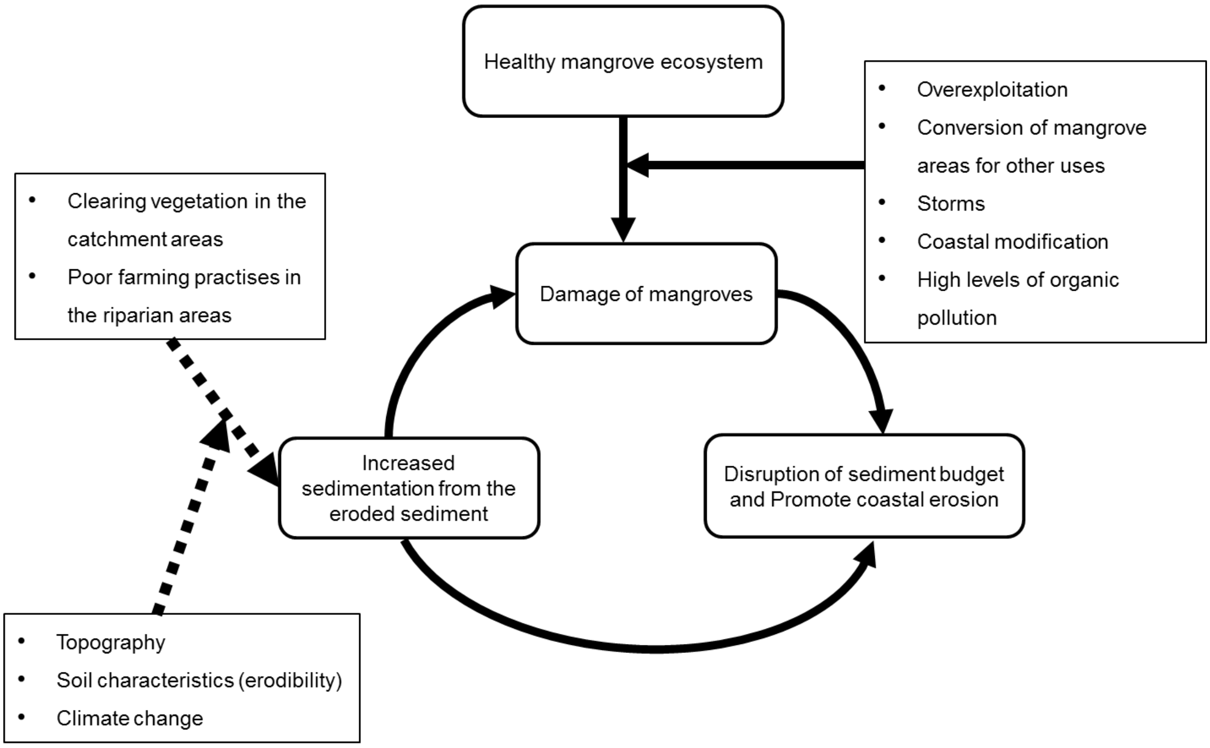


Figure 1.5 A scheme demonstrating the cycle of sediment dynamics, increased siltation and its impacts on the mangrove ecosystem. The dotted line indicates secondary causative agents. The scheme has been reproduced from a combination of literature documents (Young & Harvey, 1996; Kamaludin and Woodrofe, 1993; Hatton and Couto, 1992).

1.6.1 Documented impacts of sedimentation on mangrove trees

As mangroves trap more sediment, they contribute to the expansion of the mudflats for further colonisation (Furukawa and Wolanski, 1996). This results in higher growth rate of mangrove trees in the silted areas (Ellison and Farnsworth, 1996b; Ellis *et al.*, 2004). Since increased sediment delivery in to the mangroves has been associated with elevated nutrient levels (Alongi *et al.*, 2005), such increased tree growth may as well be attributed to the increased nutrient input as mangroves are known to respond strongly to additional nutrient input (Lovelock *et al.*, 2004). However, in a later study by Lovelock *et al.* (2007) involving nutrient enrichment and sedimentation, it was noted that nutrient enrichment only has a secondary effect and that indeed sedimentation plays the major role in increasing habitat and growth stimulation. Accretion of mineral and organic sediment within the mangrove environment may also assist the forest keep pace with the projected relative rise in sea level (McKee, 2011; Tran Thi *et al.*, 2014) this is in addition to subsurface accumulation of mangrove roots (Cahoon and Lynch, 1997; McKee *et al.*, 2007). Sedimentation has however also become a recurrent problem and is widely reported in various parts of the world (Ellison, 1998; UNEP, 1998). This is because most of the sediment brought in to the mangroves is made up of fine particles (Thrush *et al.*, 2004) and may be brought in large quantities due to increased erosion upstream (Hewawassam *et al.*, 2003).

Sedimentation particularly with fine sediments (siltation) reduces oxygen in the sediment (Thrush *et al.*, 2004) and covers the aerial breathing roots; as a result, it may impact negatively on the mangrove. The negative effects of sedimentation in mangroves range from increased seedling mortality (Terrados *et al.*, 1997; Thampanya *et al.*, 2002) over reduced growth rate (Terrados *et al.*, 1997) to interference with root aeration (Tomlinson, 1994) resulting in mature tree dieback and extensive mortality (Plate 1c and d; Ellison, 1998). In Kenya, sedimentation processes along the coastal shores had forced the shoreline of Malindi to recede by about 500 m between 1976 and 2003 (Kiara, 2003). In the mangroves of Lamu, an attempt to improve passage of the ‘Njia ya Ndovu’ Channel through dredging resulted in silting of adjacent mangroves resulting in mortality (own observation, March 2014). Increase in import of terrigenous sediments into the coast has also caused shoreline changes and habitat modification in the Athi-Sabaki estuary in Malindi (Arthur ton, 1992; Kitheka *et al.*, 2003). Massive mortality and retarded growth of mangroves were also reported in Tudor Creeks as a result of sedimentation (Mohamed, 2008).

1.7 Xylem structure and hydraulic conductance with respect to stress/ disturbance

1.7.1 Wood formation and xylem characteristics

Wood is also termed secondary xylem, the formation of which involves a succession of five major consecutive steps: cell division, cell expansion, cell wall thickening (multi-layered deposition of secondary cell wall), lignification, and programmed cell death. The entire process of wood formation may be periodic in certain cases (Mariana *et al.*, 2007) and is initiated by the activity vascular cambium which ensures the perennial life of trees through the regular renewing of functional xylem and phloem (Palomino *et al.*, 2001). Further, the activity of the vascular cambium is regulated by both genetic (internal) and environmental (external) factors (Telewiski and Lynch, 1991; Wimmer, 2002) and their continuous interaction. The anatomy of the xylem will therefore not only vary from one plant species to the other but it is also based on the prevailing environmental conditions.

The xylem is a generally complex tissue composed of xylem vessels, xylem tracheids and xylem parenchyma. Xylem has three main functions, namely; i) strengthening the plant, ii) transport of water and mineral salts and iii) acting as a storage tissue for starch (Carlquist, 2001; Tyree and Zimmermann, 2002). This study focused on xylem vessels which are structures made up of chains of elongated dead cells, forming conduits (hollow pipes) that transport sap from the roots to the leaves. The secondary walls of xylem vessels are impregnated with lignin which are hydrophobic in nature and are structurally rigid thus providing mechanical reinforcement for long distance transport of xylem sap (Weng and Chapple, 2010). The efficiency of the xylem conductivity mainly depends on its anatomical features including conduit diameters, grouping as well as frequency of occurrence (McCulloh and Sperry, 2005). Vessel grouping for instance has been found to be one of the most informative in explaining interspecific variation in cavitation resistance, P_{50}, (Scholz *et al.*, 2013). The degree of grouping among various tree species is mainly governed by sediment moisture content and is also related to the likelihood or seriousness of vessel failure by air embolism due to drought or frost (Carlquist, 1984).

Table 1.2 Xylem vessel properties of three mangrove tree species studied

Parameter	**Tree species**		
	Avicennia marina	*Ceriops tagal*	*Rhizophora mucronata*
Arrangement	Non- concentric groups of xylem tissue surrounded by internal phloem	Wood diffuse porous (no specific vessel arrangement pattern)	Wood composed of bands of earlywood (low vessel density) & latewood (high vessel density)
Grouping	Has highest vessel grouping index of the three species	In radial rows mainly of 2-3 vessels & occasionally 4 or more	In radial rows
Average diameter	54 µm	Tangential-20–50 µm	37–44 µm
Average number of vessels /mm²	43 vessels/ mm^2	77 vessels/ mm^2	45 vessels/ mm^2
Average vessel element length	0.277 mm (shortest of the three)	0.683 mm	0.407 mm

1.7.2 Sap flow in plants and xylem failure

Water transport has over many decades been explained through the cohesion – tension (CT) theory since its introduction by Dixon and Joly (1895). Despite some controversies raised (Steudle, 1995; Westhoff *et al.*, 2009), this theory is widely accepted by a great number of physiologists as an explanation to the ascent of sap in plants (e.g. Kramer and Boyer, 1995; Meinzer *et al.*, 2001; Cochard, 2002; Tyree, 2003) and constitutes the actual paradigm. It is also recommended as being consistent with the preponderance of data on water transport in plants (Brooks *et al.*, 2004). As water evaporates from the leaf surface it creates a negative pressure gradient which in turn generates a pulling force enabling sap to be transported passively from the soil to the leaves through the xylem conduits. The xylem water potential must thus be most negative at the leaves and least at the roots for water to be transported to the leaf surface (Dixon and Joly, 1895). In addition, there is the cohesion of water molecules and adhesion on the vessel walls which acts to ensure a continuous streaming of sap flow through the conduits (Tyree, 1997; Tyree, 2003).

Contrasting theory explains that water is not transported passively through the xylem conduits but rather in many small steps involving capillary, osmotic and/or transpiration bound tension gradients all operating independently (Zimmermann *et al.*, 2004; Westhoff *et al.*, 2009). As a result of the transpiration pull, xylem water remains in a metastable state due to the negative pressure (tension). Xylem water is thus always under negative pressure (tension) although mangrove trees must maintain an even more negative water potential in the xylem elements (Scholander *et al.*, 1966) to avoid back-filtration of already absorbed water into the substrate through the roots (Tomlinson 1994).

Cavitation and embolism in vessels

An efficient transport system in plants ensures continuity in sap flow from the roots to the leaves (Camacho-B *et al.*, 1974) with low flow resistance within the vessels. In the development of a water transport system, different trees species will therefore develop in such a way as to ensure the best possible compromise between most efficient transport system and safety against failure (Wheeler *et al.*, 2005; Robert *et al.*, 2009a; Manzoni *et al.*, 2013). However, the pulling force along the stem to meet the transpirational demand of sunlit leaves means that the sap remains in a metastable state (Steudle, 2001) hence vulnerable to nano-bubble being drawn into the vessel, a condition known as cavitation (Cochard, 2006). This condition will arise when xylem pressure drops below a specified threshold of (Ψ cav) which is also a function of the porosity of the pit wall (Tyree and Sperry, 1988; Christman *et al.*, 2009). The expansion of the nano-bubble to fill an entire vessel (seeding) thus preventing continuous sap flow is called embolism (Tyree and Sperry, 1989).

Cavitation and consequently xylem failure could be simply as a result of fluctuations resulting from transpiration induced loss of equilibrium within a day time scale (Meinzer *et al.*, 2009b). However, stressful conditions impose higher loss of conductive area resulting in tree mortality (McDowell *et al.*, 2008). In most literature dealing with water transport, cavitation, which may culminate into xylem failure, has therefore been associated with extreme conditions imposed by major fluctuations in soil moisture contents (drought/flooding), freeze and thaw (e.g. Ball *et al.*, 2006; Domec *et al.*, 2006; Awad *et al.*, 2010). Water potential of the atmosphere is usually already very low (negative), but may strongly vary and creating additional pulling force when the temperature rises (decreasing relative humidity). Fluctuations in the soil and atmospheric environment may be accentuated by pronounced changes brought about by human and/or natural disturbances in forests.

Implication of embolism and its reversal

Water can be passed from roots to the leaves through xylary and cytoplasmic transport, both contributing to the sum total of hydraulic conductivity (K) of a tree (Marciszewska and Tulik, 2013). Xylary resistance will therefore only affect a fraction of the process. Nevertheless, this fraction resulting in xylem failure can play a significant role in regulating plant physiological responses at all plant levels (Mencuccini, 2003). Plants therefore evolved different means as a response to problems associated with embolism including 1) by minimising chances of occurrence of cavitation; 2) by reversal once it occurs or 3) reducing its impacts. It has however been noted that although trees can adapt their xylem features or even develop resistance to cavitation under extreme environmental condition, there is a threshold which leads to catastrophic xylem dysfunction (Urli *et al.*, 2013).

Minimising occurrence chances: Trees can adapt their xylem including development of resistance against cavitation thus enabling them to grow in extreme conditions (Marciszewska and Tulik, 2013). This can be achieved through the optimal development of characteristics of the xylem hydraulic architecture in such a way as to minimise hydraulic resistance (Christman and Sperry, 2010; Jansen *et al.*, 2011) and ensure safety against embolism (Robert *et al.*, 2009a; Lens *et al.*, 2011). The characteristics include: arrangement of conduits, their frequency, diameter, the conduit wall thickness, the vessel element length and the pit characteristics. For instance it has been shown that a less efficient transport system is less prone to cavitation risk (Hacke and Sperry, 2001; Loepfe *et al.*, 2007). Different tree species have therefore evolved to either ensure efficiency of water transport or safety against cavitation depending on the risk factor. To complement these features, the leaves regulate transpiration rates under various environmental conditions to ensure that sap flow is maintained and that hydraulic failure is avoided (Meinzer and Grantz, 1990; Mencuccini, 2003). This is done in coordination with the water transport pathway upstream by constraining the xylem pressure within ranges that minimises loss of conductivity from embolism under ideal plant growing conditions (Meinzer *et al.*, 2009b). Studies have however shown that by minimising stomatal activity on sensing desiccation, plants tend to prevent hydraulic failure at the cost of carbon assimilation and this may lead to carbon starvation (McDowell *et al.*, 2008; McDowell, 2011). While certain plants may adopt a state of dormancy under such scenarios (extreme water unavailability) others maintain minimal metabolism levels but only within allowable limits after which death occurs (McDowell, 2011).

Reversal: Once a vessel conduit is embolised, there may be a tendency to refill such vessels as has been documented in a plethora of studies (e.g. Holbrook and Zwieniecki, 1999; Hacke and Sperry, 2003; Konrad and Roth-Nebelsick, 2003; Vesala *et al.*, 2003; Brodersen *et al.*, 2010). Embolism triggers the surrounding living cells to secrete solutes into the vessel creating an osmotic gradient which encourages the withdrawal of water from the adjacent fibers and parenchyma cells into the vessel (Brodersen *et al.*, 2010). Evidence of radial translocation of solutes from the phloem via rays to the axial parenchyma that have pitted connections to the embolised vessels has equally been demonstrated (Salleo, 2006; Brodersen *et al.*, 2010; Nardini *et al.*, 2011). It is also worth noting that plant species having a narrow hydraulic safety margin (which are more vulnerable to cavitation) will have a higher recovery performance via vessel refilling (Ogasa *et al.*, 2013). This gives such plants equal chances of survival as the cavitation-resistant plants when exposed to water limiting conditions.

Reduce impacts: Trees may constrain cavitation to more distal organs as a means of ensuring survival during extreme conditions thus 'sacrificing' such parts as small branches (Sperry and Pockman, 1993; Rood *et al.*, 2000). According to the segmentation theory postulated by Zimmerman (1983) and later confirmed by Choat *et al.*, (2005), there exist natural gradients in water potentials at different parts of the tree and that cavitation is more likely to occur in those sections that experience higher xylem tension. As a result, cavitation will only be confined to specified morphological regions within a tree.

1.8 Mangroves of Kenya

Kenya lies astride the equator and exhibits considerable climatic and physical variation due to difference in altitude and strong continental influence inland and marine influence to the East. As a result, a hot and humid climate generated at the coast (UNEP, 1998). The country has a coastline of about 536 km (Samoilys *et al.*, 2015) stretching from North ($1^o41'$S) to South ($4^o40'$S). The distinctive features include an almost continuous fringing reef running parallel to the coastline (UNEP, 1998 cited in Government of Kenya, 2009) and patches of mangrove forests occurring in creeks or as fringes (Ruwa, 1990; Kairo, 2001). The most extensive patch of mangroves occur in Lamu Archipelago and just south of Lamu in Tana Delta accounting for 67% of total mangrove cover (Spalding *et al.*, 2010; Samoilys *et al.*, 2015). Other smaller areas are found in Mida Creek, Kilifi Creek, Mtwapa Creek, Tudor Creek, Gazi Bay and Vanga (Figure 2.1a). The Tana River and Athi-Sabaki River situated between Lamu and Mida Creek are the major suppliers of sediment to the creeks with the latter recording a marked increase in sediment input between 1982-2007 (Snoussi *et al.*, 2007).

All mangroves of Kenya were declared as government reserved forest in 1932 and were further given protection through a gazette notice No. 174 of 1964. These forests have remained under the sole management of the then Forest Department now Kenya Forest Services (KFS) until the unveiling of the 2005 Forest Act which provides for participatory forest management through formation of community forest associations (CFAs) (Samoilys *et al*., 2015). In spite of all these, permits/ licences for exploitation of mangroves are issued irregularly against a backdrop of illegal harvesting (Kairo, 2003; UNEP, 2011). A recent estimate using Landsat data provided the mangrove area as 45,590 ha, indicating a decline of 0.7 % *per annum* between 1985 and 2010 (Kirui *et al*., 2012). The most common mangrove tree species in Kenya are *Avicennia marina* (Forssk) Vierh., *Rhizophora mucronata* Lam. and *Ceriops tagal* C.B. Rob that constitute 70% of the forest formation (Kokwaro, 1985). Less common mangrove tree species in these forests include; *Xylocarpus granatum* Koenig, *Xylocarpus moluccensis* (Lamk.), *Heritiera littoralis* Dryland, *Lumnitzera racemosa* Van Steenis, *Bruguiera gymnorrhiza* (L.) Lam. and *Sonneratia alba* J.E. Smith making up to a total of nine species (Species 2000 and ITIS). The only large stand of *H. littoralis* is found in the Tana Delta area (Spalding *et al*., 2010). A typical zonation from the open sea to the landward zone has, *S. alba*, *R. mucronata* monoculture or mixed with *B. gymnorrhiza*, *C. tagal* and finally *A. marina* in that order (Kairo, 2001). However, *A. marina* has been found to display double zonation with large trees found mixed with *S. alba* in the seaward zone in Gazi Bay (Dahdouh-Guebas *et al*., 2004a) and in Tudor Creek (Mohamed, 2008).

CHAPTER 2: The study

2.1 The species studied: *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*.

The present study focused on three mangrove tree species (*A. marina*, *C. tagal* and *R. mucronata*) commonly occurring along the Kenyan coast and which are of a general biogeographical wide range. Globally, *A. marina* has been found to be the most tolerant to low temperatures, extending outside tropical latitudes (Saenger, 2002). However, temperature is not the sole factor limiting the Southern limit of mangroves (Quisthoudt *et al*., 2013). In Kenya, these three mangrove tree species make up 70 % of the mangrove formation.

Phenology and morphology of study species –Since phenology of mangrove tree species may vary from one region to the other, the data provided is therefore based solely on studies from Gazi Bay (Wang'ondu *et al*., 2010; Ochieng and Erftemeijer, 2002). *A. marina* has leaves with green glossy upper surface and silvery white sometimes with salt-like crystals on the lower surface. The mean leaf longevity is 11 months with peak leaf emergence preceding peak leaf fall by one month. This tree species produces green fruits with large cotyledons whose skin slowly turns light yellow and wrinkly at maturity with a peak season from April to May. *C. tagal* has a peak fruiting season in February to March but propagules are always available during most times of the year. This species produces long slender propagules which turn from green to brown-green with yellow collar during maturity. *R. mucronata* has elliptical leaves with mean longevity of 12.8 ± 1.2 months. The species produces long relatively plump propagules (Plate 2.1) which peaks in March to June. Its bud initiation is seasonal and may vary between natural and reforested mangrove areas. More information of the description of these tree species is given summary in table 2.1.

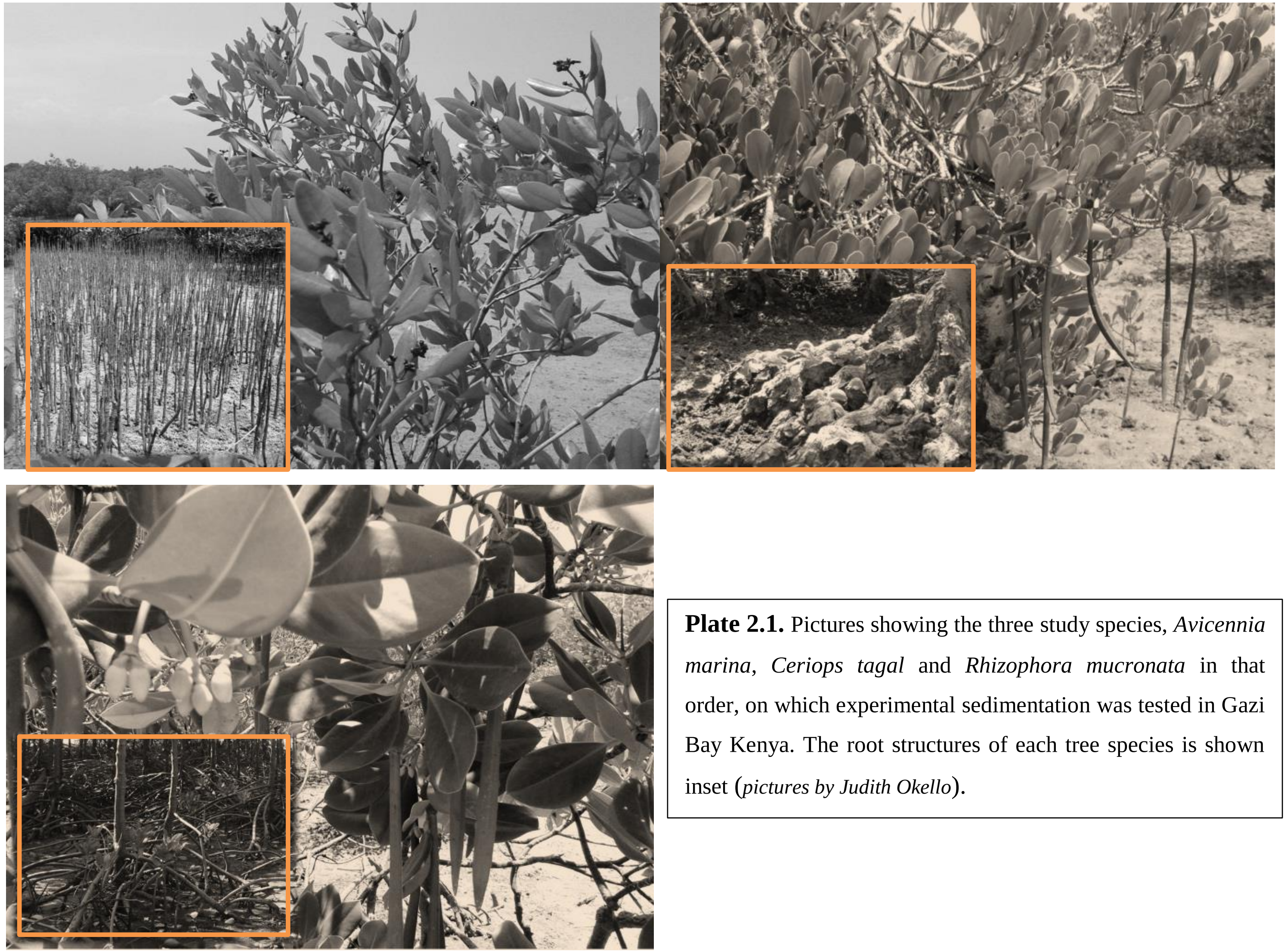


Plate 2.1. Pictures showing the three study species, *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata* in that order, on which experimental sedimentation was tested in Gazi Bay Kenya. The root structures of each tree species is shown inset (*pictures by Judith Okello*).

Table 2.1 Description of the three mangrove tree species studied

Attribute	**Tree species**		
	A. marina	***C. tagal***	***R. mucronata***
Family	Acanthaceae	Rhizophoraceae	Rhizophoraceae
IUCN Red list	Least concern [1].	Least concern [1]	Least concern [1].
Architecture	May grow as a shrub (only 3 m tall), or tree (up to 14 m) in highly productive estuarine systems [2]. In Kenya, heights of up to +20 m have been reported [*]	Small shrub or tree (6 m tall), occasionally 15 m [2, 3]. Can attain 1.5 m height in under vigorous growth conditions [**].	Erect, growing up to 27 m [2,3]
Position in the tidal flat	Wide range of occupancy within the tidal flat, found to display double zonation (more than one inundation class). [4, 5]	Restricted to mid intertidal zone (inundation class 3 and occasionally 2 [5]. Classes as per [***])	Restricted to inundation class 2 and occasionally 3. [5]
Vivipary	Cryptovivipary: the embryo displays no dormant phase. [6]	True vivipary. [6]	True vivipary. [6]
Dispersal strategy	Has high fecundity (Clarke, 1992); Propagules remain viable for long period of time (Clarke, 1993); Compact, and hence less susceptible to root retention [+].	Produce many propagules that disperse fast and potentially over long distances. [7] Production of vertically and horizontally floating propagules, the former being less affected by ambient wind currents over their dispersal trajectory [+, ++]; Long term viability [+++].	Produce fewer but fast anchoring propagules [7]; Propagules float vertically & horizontally, the former being less affected by ambient wind currents over their dispersal trajectory [+,++]; Long flotation period and viability [^]; Seaward position of parent trees, reduce distance to open water thus lowering retention potential & predation in the forest.
Salt elimination	Secretion through salt glands in the leaves. [8]	Accumulate excess salts in senescing leaves and dead bark. [8]	Accumulate excess salts in senescing leaves & dead bark. [8]
Aerial Roots	Are short often < 30 cm, spongy and lenticel equipped (pneumatophores). May grow taller under increased hypoxia. [9, 10]	May not be always well developed (knee roots) but are more pronounced in wetter areas where growth is more vigorous. [8]	Branched, looping and grow from the lower trunk (prop roots). [8, 11]
Cable roots	Present and enhance diffusion of oxygen creating an oxic zone around the rhizosphere. [12]	Not always well developed. [8]	Absent. [8]
Sediment retention	Retains 30% of the sediment coming in to the system due to negative geotropic nature of pneumatophores. [13]	Lower than that retained by *Rhizophora*. [13]	Retains up to 20% of the suspended sediment brought in to the mangroves. [11, 13]
Uses	Inferior firewood used for fish smoking, brine boiling & lime production. Building dugout canoes, beehives, leaves as fodder. [14]	Fuelwood with high calorific content, building poles, fencing posts, making fish traps, bark for dye, boat making. [14]	Fuelwood with high calorific content, building poles, fencing posts, making fish traps, bark for dye. [14]
Growth layers	Not annual/ seasonal. Form through successive cambia division resulting in a patchy structure due to lack of synchrony. [15, 16]	Concentric rings with indistinct borders marked by gradual change in vessel density and occasionally narrow parenchyma bands. [17, 18]	Annual growth bands of alternating high & low vessel density zones borders indistinct marked by gradual transition in vessel density. [19]
Vessels	Higher vessel density than *Rhizophora*, elements narrower & shorter. Features that ensure safer hydraulic architecture. [20]	Vessels occur in radial multiples of 2-6 sometimes solitary. [18]	Vessel densities governed primarily by rainfall and inundation as well as vary along salinity gradients. [21, 22]

Source: [1] (Polidoro *et al.*, 2010), [2] (Aksornkoae, 1993), [3] (Whitman, 1989), [**] (Kairo *et al.*, 2002), [4] (Dahdouh-Guebas *et al.*, 2004a), [5] (Robertson and Alongi, 1992), [***] (Watson, 1928), [6] (Kathiresan and Bingham, 2001), [+](Van der Stocken, unpublished data), [7] (De Ryck *et al.*, 2012), [++](Van der Stocken *et al.*, 2013), [+++](Clarke *et al.*, 2001), [^](Drexler, 2001) [8] (Tomlinson, 1994), [9] (Ishshalomgordon and Dubinsky, 1992), [10] (Dahdouh-Guebas *et al.*, 2007), [11] (Furukawa and Wolanski, 1996), [12](Marchand *et al.*, 2004), [13] (Kathiresan, 2003), [14] (de Lacerda, 2002), [15] (Schmitz *et al.*, 2008), [16] (Nazim *et al.*, 2013), [17] (Okello, 2008), [18] (Robert *et al.*, 2010), [19] (Verheyden *et al.*, 2004), [20] (Robert *et al.*, 2009a), [21] (Verheyden *et al.*, 2005), [22] (Schmitz *et al.*, 2006).

2.2 The study sites

The study was conducted in two different mangrove forests along the Kenyan coast – Gazi Bay and Mtwapa Creek (Figure 2.1a). Both sites experience the coastal climate characterised by bimodal distribution of the precipitation. A distinct dry season (January - February) is followed by a long (April - July) and a short (October - November) rainy season (Figure 2.1b).

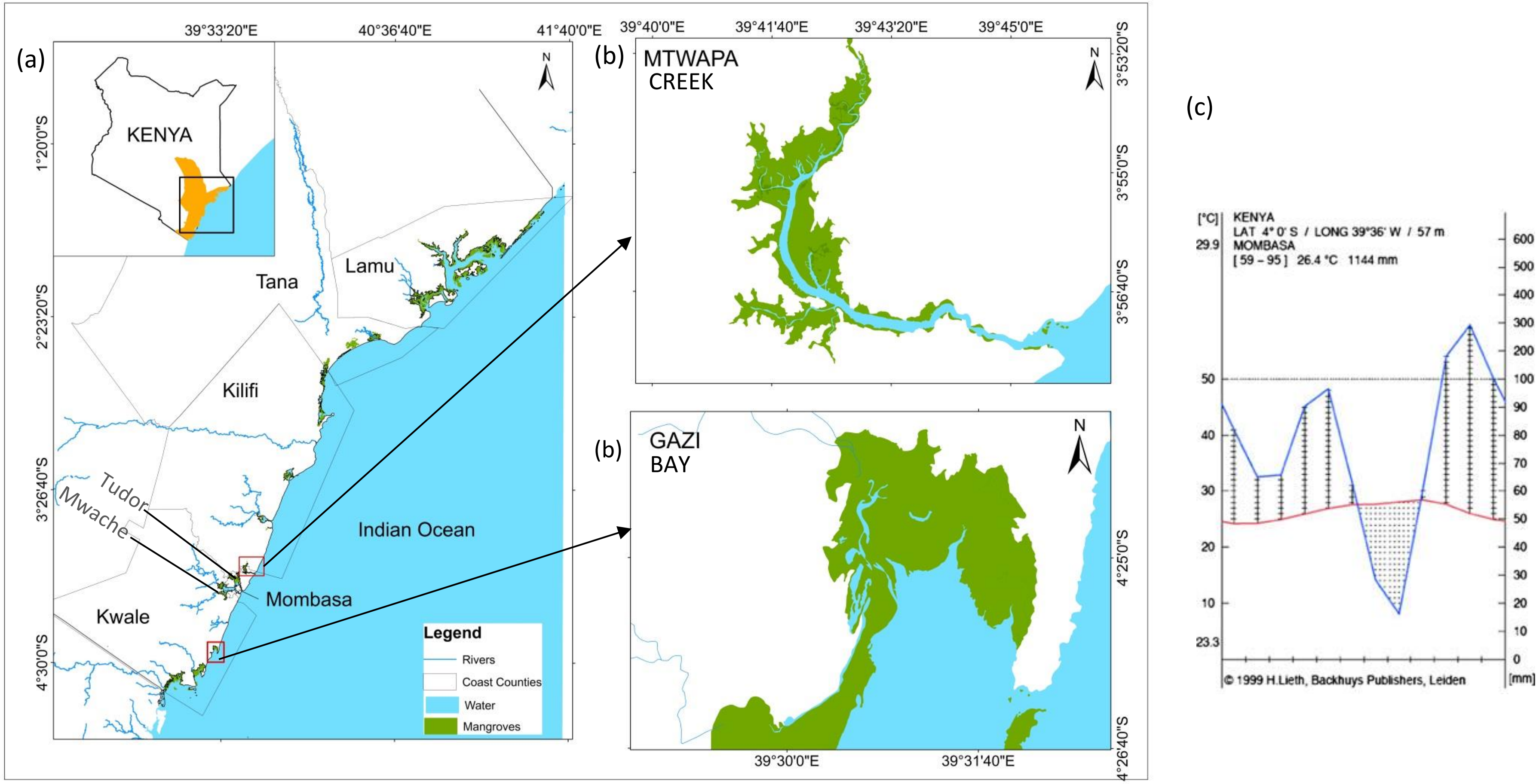


Figure 2.1. **a**) Map of the Kenyan coastline locating the two study areas marked with red rectangles with inset.the coastal counties highlighted in a map of Kenya b) Map of the two study sites Mtwapa Creek (top) and Gazi Bay (bottom) **C**) Climate diagram of Mombasa town (Lieth *et al*., 1999).

The average temperature at the Kenyan coast ranges from 22 to 30°C, with a mean relative humidity from 65% to 81% (Kenya Meteorological Department).

Part one of the study (involving surveys) was conducted in Mtwapa Creek (39°44′E, 3° 57′S), which is situated at the boundary of Mombasa (south) and Kilifi (north) counties. The creek is adjacent to Mtwapa town and lies about 13. 5 km as the crow flies north from Mombasa city (Figure 2.1b). Notwithstanding the high population growth rate in Mombasa and Kilifi counties (3.9%), Mombasa and Mtwapa just like other towns in these counties, both experience net immigration of people from upcountry attracted by employment in the tourism sector and other industries including the port (Government of Kenya, 2007). The two counties have therefore the highest coastal urban population accounting for 69% of the total individuals living in urban areas in the region (Government of Kenya, 2007; Government of Kenya, 2009). The area around Mtwapa Creek has seen an increase in built up area from a low level of approximately 32 ha (0.6%) in the 90's to 347 ha 5% in 2009 (Bosire *et al.*, 2015). There are also major hotel developments and tourist settlements along the creek. At the mouth, the creek receives untreated sewage from underground seepage of septic tanks, nearby beach hotels, recidences, Shimo la Tewa prison and Mtwapa Municipality (Mvoyi 2004; personal observation). Drainage systems within the municipality are also poor resulting in storm run-off waters flowing directly into the creek (Mutual *et al.,* 2004). The entire Mtwapa Creek together with the adjacent Tudor Creek are both under the Nyali-Bamburi-Shanzu pilot site which were delineated for administrative purposes of Integrated Coastal Management (ICM) process to address coastal resource use and management (McClanahan *et al.,* 2005).

The creek is approximately 13.5 km in length and opens to the Indian Ocean through a long narrow channel (Figure 2.1b). It consists of three forest patches (Gung'ombe, Kitumbo and Kidongo, all named after adjacent large villages) which are situated further landward from the mouth (Figure 2.1b) and fed by three seasonal rivers (Kwa Ndovu, Kashani and Kidutani). There are steep slopes (covered with arable lands and a few patches of thickets and occasionally residences) facing the mangroves on both sides of the creek. The tidal range in Mtwapa Creek is high relative to the depth (Mutua *et al.,* 2004). The mangrove forest has been said to had earlier been said to have eight out of nine of the mangrove species found along the Kenyan coast (Mirera and Mtile, 2009).

Part two which was the experimental phase of this study was set-up in Gazi Bay. The bay is characterised by the presence of eastern and western creeks, fringing reefs, and two seasonal rivers - Kidogoweni and Mkurumuji that drains into the ocean. Ground water seepage has also been reported though is restricted to a few locations (Tack and Polk, 1999).

Mangroves of Gazi have been widely studied in the past (as well as in the present) and base data on the physicochemical parameters are readily available e.g. salinity ranges (Robert *et al.*, 2009b), redox and sulphide (Matthijs *et al.*, 1999), hydrodynamics (Kitheka 1997). It was also only in this area that substantial coverage of plantations of all the three study species could be found in the same locality hence minimising local differences during running of the experiment. *Ceriops tagal* plantations used in the present study were established in 1994; while *Rhizophora* and *Avicennia* plantations were established in 2000 and 2006 respectively. Like other mangroves along the coast, mangrove exploitation for wood is rampant in Gazi; with clear cut areas and no regeneration still evident in areas which were mostly harvested in 1970s to provide fuel for the chalk, limestone and brick industries in Kenya (Kairo, 1995). These are among the areas where *A. marina* and *C. tagal* plantations used in this study had been established. *Rhizophora mucronata* was replanted after the 1997 - 1998 El Niño rains which led to massive flooding in Kenya resulting in mangroves mortality in the study area and other mangrove areas along the coast (Kitheka *et al.*, 2002; Ongwenyi and Mavuti 2002). Initial replanting of the species was carried out to match with the natural location of the species. All plantations in Gazi were established by the Kenya Marine and Fisheries Research Institute (KMFRI) and are currently reserved as Permanent Sample Plots (PSP) by KFS.

Gazi Bay experiences a semi-diurnal tidal regime with an amplitude of ca. 4.0 m at spring tide and 0.7 m at neap tide (Hemminga, 1994) and short tidal reside times of 3-4 hours (Kitheka, 1997). The mangrove forest covers an area of about 600 ha (UNEP, 2001; Neukermans *et al.*, 2008) with all the nine mangrove tree species reported in Kenya represented. When compared to the Mtwapa pilot area, the mangrove forest in Gazi is relatively pristine considering the relatively low population in the adjacent villages (Figure 4a) and the better enforced management. Additionally, being in a rural setting, there are no major developments in the area with the nearest small town (Msambweni) situated about 5.4 km away as the crow flies from Gazi village.

2.3 Study rationale

As the world population increases and since the onset of industrial revolution, several human-resource conflicts have arisen gradually diminishing the self-regulation capacity of natural resources. Coastal areas for instance are now home to more than half of the world's population and much of the world's economic output is related to the coastal resources (Cicin-Sain and Belfiore, 2005; McGranahan *et al.*, 2007). Attracted by the economic activities taking place in coastal and ocean areas (such as shipping, oil and gas development and coastal tourism), more people migrate to the coastal cities thus exerting more pressure to these resources hence putting their value and productivity at risk (Government of Kenya, 2009). The mangrove ecosystem is one of such coastal resources in which natural functionality balance has been continuously disrupted by human activities due to increased pressure. The primary issues affecting mangroves are further compounded in peri-urban mangroves where human population is even higher and multifaceted activities are on-going. Coupled by influence of harsh weather conditions and climate change, mangrove ecosystems may face further degradation.

For a long time, scientists working in the mangrove environment have emphasised the ability of mangrove trees to cope with various forms of otherwise unfavourable conditions including temperature, elevated salinity levels, flooding, and harvesting regimes among others (Schmitz *et al.*, 2008; Robert *et al.*, 2009a; Feka *et al.*, 2011; De Ryck *et al.*, 2012; Quisthoudt *et al.*, 2013). Although influence of increase in the degree of sediment accumulation has also been assessed (Terrados *et al.*, 1997; Ellison, 1998; Thampanya *et al.*, 2002; Ellis *et al.*, 2004; Vaiphasa *et al.*, 2007), the experimental studies have mostly been on young seedlings. One might therefore postulate a stronger capacity for an acclimative plastic response in larger, well-established trees. This brings up the question of how physiological activities of affected trees would be impacted and how they respond morphologically and anatomically to sedimentation.

The current study involved: (i) analysing the structural status of the peri-urban mangroves of Mtwapa Creek; (ii) assessing the perception of the local communities on status of mangrove forest against a backdrop of their activities in the hinterland and mangrove usage patterns; (iii) casting light on the influence of sedimentation on crown foliage dynamics, hydraulic conductivity, xylem structure, and root and bark development of affected trees. We conducted structural surveys in the mangrove forest of Mtwapa Creek potentially impacted by disturbance from urban expansion, population growth and other human activities in the vicinity.

We then carried out an experiment in mangrove plantations of known age in Gazi Bay to understand the sedimentation tolerance threshold and its impact on selected physiological processes and anatomy of mangrove trees.

1b.3.1 Objectives

Disturbance can take various forms and are characteristic of any ecosystem including mangroves. When maintained within certain allowable limits (Figure 1.4), disturbances permits maintenance of a given stable state which is equivalent to resilience hence the ecological status is not compromised. Disturbances may disrupt the natural balance of processes within such ecosystems including changes in sediment budgets and salinity and tidal regimes. As such, it may trigger a series of responses in tree establishment and development. While such responses may be displayed in loss of stability of a forest and may culminate in irreversible degradation of the system, disturbances could also result in improved performance of physiological processes and consequently tree growth. It may equally lead to the development of adaptive mechanisms to counteract the resultant otherwise stressful effects. Sediment accretion is one of the important natural processes within the mangrove environment particularly in the face of relative sea level rise. In each case, sediment fluxes are gradual and while the trees thrive from the benefits of terrestrial sediment, the system ensures balance in elevation for possible sea level rise scenario. However, abrupt and/or rapid sediment input leading to partial burial of the trees may be detrimental to the trees development in the short term and the entire ecosystem in the long run. But how are ecophysiological processes affected before the mangroves trees die from partial sediment burial? What is the threshold below which normal tree functioning is ensured.

The **main objective of this study** was to understand the impacts of disturbance on mangrove trees, as individuals and as an assemblage. Specifically the study targeted large sedimentation on selected ecophysiological processes (phenology, water transport), root development and general physiognomy and hence its impact on wood formation in mangroves. A survey was also done on the extent of wood exploitation and other human activities, in order to obtain background information on the environmental management in the area and hence to help create an integrated picture of the evolving mangrove ecosystem in the human-nature context.

Main question: What is the significance of sedimentation in shaping the ecological status of mangrove forests?

The main objective and derived main question has been subdivided in **specific objectives**, which are best reflected as hypotheses, underlying this work.

Hypotheses

Ho1: Natural regeneration is sufficient to sustain the peri-urban mangrove forest of Mtwapa Creek.

Ho2: Perception by the local communities on mangrove state identifies the ecosystem sustainability or the factors important for sustainability

Ho3: Partial burial of mangrove trees results in similar responses in *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*.

Ho4: Partial burial does not significantly alter the phenological cycle and productivity of affected mangrove trees.

Ho5: Burying mangrove trees lowers hydraulic conductivity because alterations in xylem and stomatal properties (if any) can not occur as an immediate response.

Ho6: Burying mangrove trees does not alter root and bark development in affected trees.

1b.3.2 The study approach

The study looks at disturbance from two perspectives, (i) as it occurs in nature and (ii) projected large forms of disturbance as a result of increased anthropogenic pressure and climate change related events. Since most mangrove studies have focused on local patterns other than an integrated approach, the current study begins by taking a look at disturbance from distal areas, putting in to focus a case of most potentially disturbed mangrove forests (peri-urban context). For purposes of integration in management, the perception of the local community and possible influence of economic activity on the mangroves of Mtwapa Creek is evaluated. We apply a physiological and anatomical approach using experimental set ups to answer to the question on whether or not sedimentation would play a significant role in shaping the forest structure of a mangrove forest. Since Mtwapa Creek mangroves are assumed as affected, a relatively pristine forest of known age is selected in Gazi Bay for the experimental set-up to minimise confounding factors on a baseline of a forest that has not received human impact by exploitation or sedimentation yet. The broad study question is tackled in a systematic manner where an answer in a preceding section forms the question in the next (Figure 2.2).

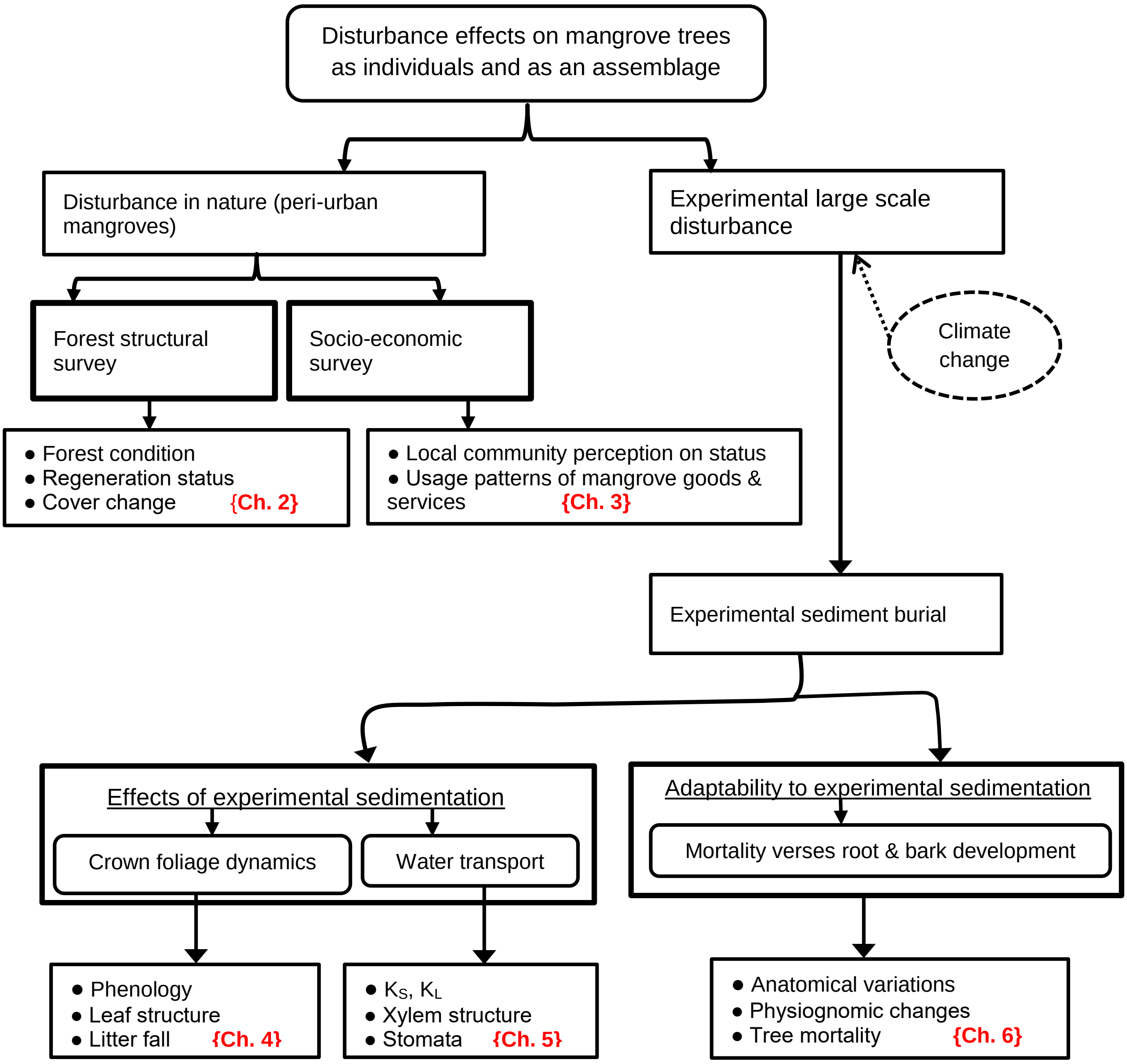


Figure 2.2 A flow chart outlining the structure of the thesis with emphasis (bold text boxes) made on the major aspects covered, towards assessing the effect of disturbance on mangrove trees as individuals and as an assemblage. Climate change is an external factor affecting the system but is not directly addressed.

.

PART II

The mangroves of Mtwapa Creek

Pictures taken in Mtwapa Creek in February 2011 by Nico Koedam

CHAPTER 3:

Self-sustenance potential of peri-urban mangroves: a case of Mtwapa Creek Kenya

Adapted from
Okello J.A., Schmitz, N., Kairo, J.G., Beeckman, H., Dahdouh-Guebas, F., Koedam, N., 2013. Self-sustenance potential of peri-urban mangroves: a case of Mtwapa Creek Kenya. Journal of Environmental Science and Water Resources 2 (8), 277 - 289

Abstract

Background: Mtwapa Creek mangroves are situated in the vicinity of the populous town of Mtwapa and are surrounded by local communities living in the villages along the creek. Both elements pose potential pressure on these peri-urban mangroves hence compromising their sustainability and ability to support coastal livelihoods.

Objectives and methods: This study evaluated the sustenance potential of Mtwapa Creek mangroves based on mangrove cover change, forest structural status and natural regeneration. This was carried out through assessment of tree abundance, dispersion pattern and natural regeneration status along belt transects in three forest patches (Gung'ombe, Kitumbo and Kidongo) in the creek and cover change analysis of the area over 10 year period before the survey.

Results: Cover change analysis for the 10 years preceeding this study showed increases in mangrove forest cover. However, the studied sites were characterised by high stem densities with low basal areas, low utilisation classes and poor forms (poles requiring modification before use or unsuitable for construction accounting for 75% of the total stem density). Natural regeneration varied among species with *Avicennia marina* having low survival rates while the other species achieved ≈100% recruitment to successive regeneration classes.

Conclusion: Mtwapa Creek mangrove forest may be having adequate natural regeneration but poor tree development hence compromising the forest's self-sustenance. Additionally, proximity to human settlement largely contributed to selective harvesting hence influencing the forest structure.

Contributors: Okello J.A. – main author; Schmitz N. – write-up, Kairo J.G. – supervision, Beeckman H. – co-promoter; Dahdouh-Guebas F. – promoter, Koedam N. – lead promoter, study design and supervision. Others: Choge S. – mapping, field data collectors from KMFRI and KFS (as in acknowledgement).

3.1 Introduction

Mangroves form an ecotone between land and sea, and as such undergo constant natural disturbance due to the tidal cycles and its corollaries. Catchment processes (Kitheka *et al.*, 2002), global change and the multiple uses of mangroves set against the backdrop of increasing demographic pressure in most coastal areas, only worsening the situation (Cicin-Sain and Belfiore, 2005). The coastal region of Kenya (Figure 2.1) for instance has a population the growth rate >3% which is considered high as per international standards (Government of Kenya, 2009). There is thus always a readily available market for mangrove wood which caters for 70% of the local population's wood requirement (Wass, 1995). With no management plan in place to put a check on the licenced cutters, some mangrove forest patches in Kenya have been completely degraded as a result of overexploitation (Bosire *et al.*, 2003; Dahdouh-Guebas *et al.*, 2004b; Bosire *et al.*, 2013).

Other than overexploitation, peri-urban mangrove forests may face further degradation due to lack of planning and uncontrolled development in the shoreline and beach areas intended for tourist attraction (White *et al.*, 2005), as well as urban expansion necessitated by rapid population growth (Cicin-Sain and Belfiore, 2005). In Kenya and other developing nations, these mangroves also face the problem of pollution from direct discharge of domestic sewage from point sources into the mangrove forest especially at Tudor and Mtwapa Creek (Government of Kenya, 2009). It is in line with these multiple stressors that mangrove structural surveys are conducted to understand ecological status of the forest and hence act as a basis for making management decisions.

Site specific survey is especially important in the current legal provision (Forest Act 2005) in Kenya in which mangroves have been divided into blocks being managed by Community Forest Associations (CFAs). Moreover, forest disturbances tend to be localized rather than a large scale phenomenon and as such vegetation structure may widely vary from one forest area to the other (Hubbell, 1979). In addition, even within the same regions, forest areas may display strong differences in zonation (Dahdouh-Guebas *et al.*, 2002). In this section of the study, the status of both mature trees and natural regeneration of Mtwapa Creek mangroves was assessed to determine the self-sustenance potential of the forest. Results of tree abundance, dispersion pattern and natural regeneration as well as cover change of the forest are presented.

3.2 Materials and Methods

3.2.1 *Study area*

The study was carried out in Mtwapa Creek (39°44′E, 3° 57′S), within three forest patches (Gung'ombe, Kitumbo and Kidongo, all named after adjacent villages) which are situated further landward from the mouth (Figure 3.1).

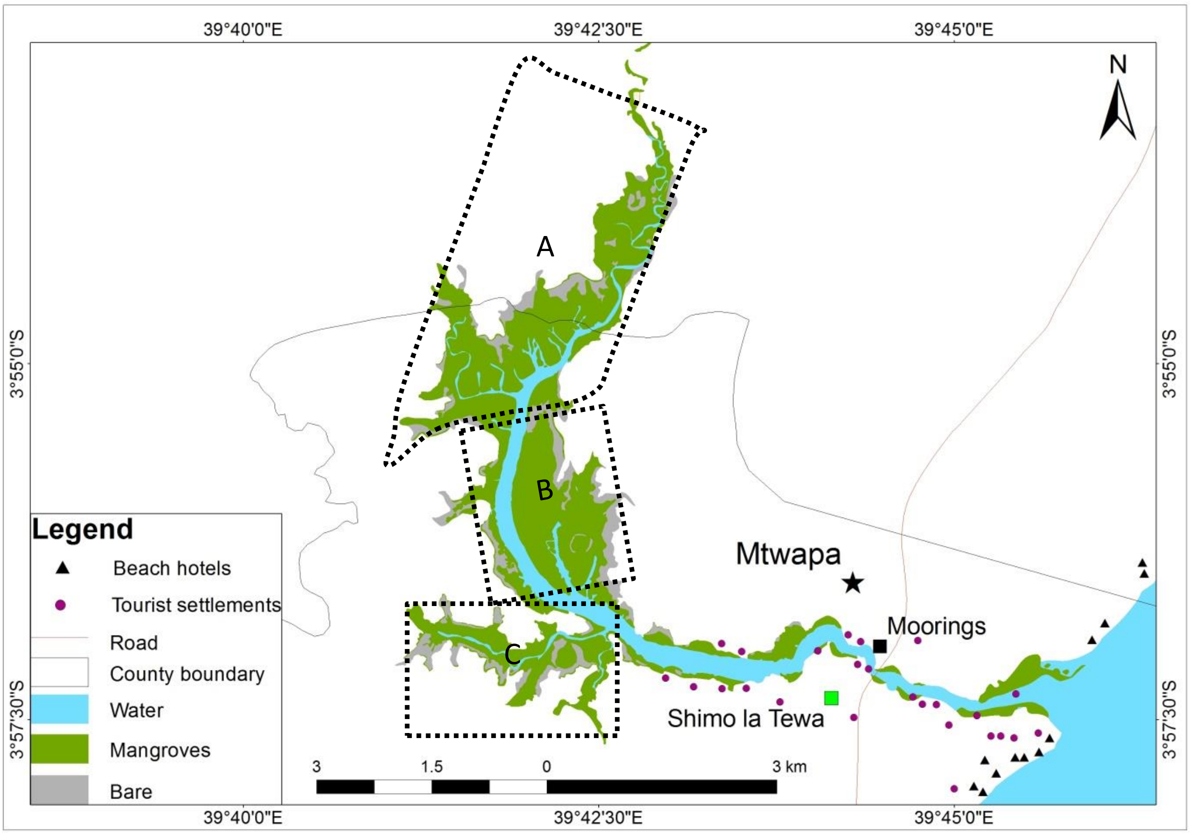


Figure 3.1 Map of Mtwapa Creek (red box) showing the forest patches A- Kitumbo, B-Gung'ombe and C-Kidongo where the structural survey was conducted in 2010 March, delineated using doted lines (Source KMFRI database).

3.2.2 *Field measurements*

In March 2010, a reconnaissance survey and examination of aerial photographs of the area (see appendices Figure S1) was carried out in order to determine the position of transects (Kairo *et al*., 2002). Ten-meter wide belt transects were laid across each forest patch from vegetation edge landward to the water line to ensure that mangrove zonation along tidal flat if any is captured. In each of the transects, 10 m x 10 m quadrats within which sampling was done were established after every 200 m. The number of transects and hence quadrats was determined by the size of each of the forest patch. Where complete transects could not be laid due to difficulty of access, spot sampling involving random placement of extra quadrats with dimensions as those within the belt transects was done to ensure proper coverage of the entire forest area. Table 3.1 gives a breakdown of the sampling area.

Table 3.1 sampling design showing number of quadrats laid in each of the 3 forest patches.

Forest patch	Transects laid	Quadrats in transects	Spot sampling quadrats	Total quadrats
Gung'ombe	5	20	6	26
Kitumbo	7	32	7	39
Kidongo	4	10	3	13
				78

All mature trees with a butt diameter greater than 2.5 cm were marked in each quadrat. Heights (ht) of the identified trees were measured using a Suuntoclinometer, while stem diameters at 130 cm above ground (D_{130}) were measured using a forest calliper (sensu Brokaw and Thompson, 2000). D_{130} was measured in all species except for *Rhizophora mucronata* Lamk. (Rhizophoraceae), where stem diameter was measured 30 cm above the highest prop roots due to the architectural complexity of the genus (Dahdouh-Guebas and Koedam, 2006). In cases where the stem forked below 130 cm (for example, *Avicennia marina* (Forssk.) Vierh. (Acanthaceae) and *Sonneratia alba* (Sm.) (Lythraceae), the individual 'branches' in a clump were treated as separate stems.

Pole usability in construction (quality) was assessed based on the form of the lead stem and assigned either form 1, 2 or 3. Form 1 stems denote those whose lead stem is straight and excellent for construction. Form 2 stems require slight modification before they are used for construction while the poles that were unsuitable for construction were assigned form 3 (Kairo, 2001). Percentage vegetation cover per quadrat was estimated based on visibility of the sky from the forest floor as perceived by three independent observers (Zhou *et al.*, 1998). Stumps and standing dead trees were also counted in each quadrat as an indicator of exploitation and tree mortalities. Stumps were graded as either old or new based on whether or not they were from recent cuttings.

All trees with D_{130} below 2.5 cm were put under the category of natural regeneration and termed saplings (Kairo *et al.*, 2002). The number of different species of saplings was determined in sub-plots of 5 m x 5 m, within the 10 m x 10 m quadrats. The saplings were further grouped according to height classes (Kairo *et al.*, 2002) where those less than 40 cm height were classified as regeneration class 1 (RCI). Regeneration class 2 (RCII) had heights between 40 and 150 cm, while all small trees with heights greater than 1.5 m but less than 2.5 cm diameter were grouped as Regeneration class 3 (RCIII).

3.2.3 *Canopy change detection*

To determine cover change over the past ten years from the time of sampling (structural survey), two cloud free Landsat images of 2000 and 2010 with pixel size of 30 m of the study area were downloaded from the USGS web-site (http://glovis.usgs.gov/). The Landsat imageries downloaded are geometrically system corrected (UTM Zone 37, WGS 84). Image classification for the two images was done in ArcGIS 10 software using the supervised method which implies that each cell in the study area is assigned to a known class. Five cover classes; water, bare land, dense and sparse mangrove forest, and terrestrial vegetation were used in the classification and the resultant shape files saved as kml. Forty five (45) reference points (Ground control points) obtained from the structural survey were plotted in ArcGIS and the map exported as kml to Google Earth @2015 imagery. The shapefiles obtained were exported and overlaid on the Google Earth image to validate the cover classes and identify how well they matched high-resolution imagery.

3.2.4 *Analysis of terrain of the riparian area*

Google Earth, TCX converter and ArcGIS 10 were used to determine the terrain of the area adjacent to the mangrove ecosystem. A polygon was drawn around the entire mangrove area with a buffer extending 5 - 6 km into the adjacent land (Figure 3.2). A path was then drawn as shown in figure 3.2 then saved and imported into the TCX program to convert the digitised points into readable elevation/ altitude values and then exported into an Ms Excel sheet. In ArcGIS, the data was plotted and a triangulated irregular network (TIN) created, which is the surface upon which the contours were interpolated. A contour map of the digitised area is then generated automatically.

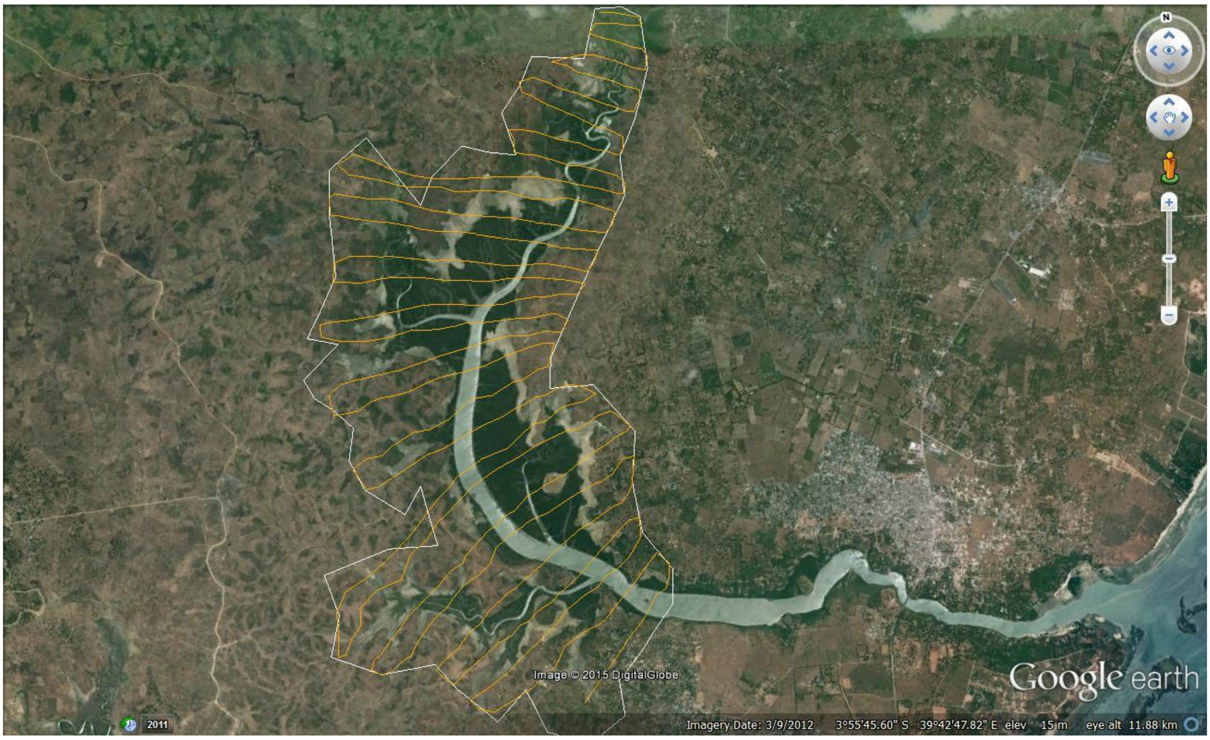


Figure 3.2 Google Earth image showing the polygon drawn around the mangrove area and the path (yellow colored lines) followed during the digitisation process to extract the elevation data.

3.2.5 *Data treatment*

All the analyses were based on assumptions that; (a) natural regeneration represents the future forest and, (b) in the process of development natural regeneration will in turn experience the same level of disturbances as depicted by the status of the current standing mature trees. This is complemented by canopy change analysis to capture past losses or gain in terms of mangrove cover. Data analysis and graphical presentation were carried out using Ms Excel and STATISTICA 8.0. After testing for homogeneity of variance using a Shapiro-Wilk's W test, a Kruskal-Wallis (a non-parametric test) was performed on stem densities of different size classes. A Mann-Whitney U Test was used to determine if any correlations existed between vegetation cover per area sampled and stumps left as a result of cutting. Regeneration densities and ratios were calculated and correlation with canopy gaps done using Spearman rank correlation.

Structural attributes

Tree basal area (Ba, m² ha^{-1}) and stand density (De, stems ha^{-1}) (Mueller-Dombois and Ellenberg, 1974; Cintrón and Schaeffer-Novelli, 1984), were derived using equation 1A and 1B. Relative values of density, dominance and frequency were estimated using equations 2A, 2B and 2C (Dahdouh-Guebas and Koedam, 2006). The ecological importance (IV) of each species was calculated by summing its relative density, relative frequency and relative dominance (Curtis, 1956; Cintrón and Schaeffer-Novelli, 1984). The species with the highest IV in the population becomes the principal species.

$$\underline{\text{Basal area}}\ (\text{Ba}) = \sum_{i=1}^{m} \sum_{j=1}^{ni} \frac{Baij}{ni} \tag{1A}$$

$$\underline{\text{Stand density}}\ (\text{De}) = \sum_{i=1}^{m} \frac{1}{(\sum_{j=1}^{ni}(\frac{dij}{ni}))^2} \tag{1B}$$

$$\underline{\text{Relative De}}\ (\text{De}_\text{r}) = \frac{100ni}{\sum_{i=1}^{m} ni} \tag{2A}$$

$$\underline{\text{Relative dominance}}\ (\text{Do}_\text{ri}) = \frac{100Bai}{Ba} \tag{2B}$$

$$\underline{\text{Relative frequency}}\ (\text{F}_\text{ri}) = \frac{100Fi}{\sum_{i=1}^{m} Fi} \tag{2C}$$

$$\text{Ecological Importance (IV)} = \text{De}_\text{r} + \text{Do}_\text{ri} + \text{F}_\text{ri} \tag{2D}$$

where: $\boldsymbol{n_i}$ is the number of trees sampled for a given species; $\boldsymbol{i}$; $\boldsymbol{j}$, is the tree number, **Ba*ij*** is the basal area of first tree to the last one; **m** is the number of species; $\boldsymbol{F_i}$, is number of quadrats in which species $\boldsymbol{i}$ is represented, multiplied by 100.

Stems of mature trees were further grouped into utilisation classes with different categories of sizes for inventory purposes. The naming of the classes is in Kiswahili language and refers to different uses of the poles. The classes include; *fito*, *pau*, *mazio*, *boriti*, *nguzo*, and *vigingi* with diameter ranges of 2.5 – 3.5 cm, 4.0 – 7.5 cm, 7.5 – 11.5 cm, 11.5 – 13.5 cm, 14.0 – 20.0 cm, and 20.5 – 35.0 cm respectively (Roberts and Ruara, 1967). An extra class, '*mbao*', with D_{130} greater than 35 cm was also included in this study, to cater for large *Avicennia marina* trees.

Morisita dispersion index

Dispersion was determined using Morisita's dispersion Index $(\mathbf{I_\delta})$ (Morisita, 1959). This was based on the analysis of spatial pattern of adults and saplings carried out in the 10 m x10 m quadrats along a single transect. The selected transect in each case has to have a representation of all the species encountered in a given forest patch.

$$\text{Morisita index } (\mathbf{I}_\delta) = \boldsymbol{q'} \times \boldsymbol{\delta} \qquad (3A)$$

$$\boldsymbol{\delta} = \frac{\sum_{i=1}^{i=q'} \boldsymbol{n}(\boldsymbol{n}_i - \mathbf{1})}{\boldsymbol{N}(\boldsymbol{N} - \mathbf{1})} \qquad (3B)$$

$$\boldsymbol{\Sigma n}\ (\boldsymbol{n}_{i,}\text{-}\mathbf{1}) = \Sigma n^2 - N \qquad (3C)$$

where: ***q'***, is the number of quadrats within the selected transect; $\boldsymbol{n}_{i,}$ is the number of individuals per species in the i^{th} quadrat, and ***N***, is the total number of individuals in all ***q'*** quadrats. If $I_\delta > 1$, the population is clustered, if $I_\delta < 1$, the population is randomly dispersed and if $I_\delta = 1$, the population is evenly dispersed.

Shape of the population distribution

For predictive purposes in forest management, it is often desirable to understand the shape of the underlying distribution of the population. A forest is usually assumed to be stable when a given D_{130} distributions can be maintained over a period of time. This allows a given harvesting schedule to be maintained repeatedly without compromising stability and as such considered to be sustainable (Sterba, 2004). Most management schemes of uneven-aged forest strive to attain a reverse-J shaped curve as a way of ensuring stability (Ducey, unpublished). De Liocourt's model which was used to harmonise stand densities in this study is one such example. De Liocourt's model is based on the assumption of a constant "q" obtained as a ratio of successive diameter classes (Equation 4). According to this model, the ratio between the number of trees in successive diameter classes of uneven aged stands is approximately constant for a given forest (Clutter *et al.*, 1983; Cancino and Von Gadow, 2002; Mohamed, 2009). This model has been popularised in several studies due to the fact that it allows comparison of different silvicultural treatments in relatively simple terms (Meryer, 1952; Sammi, 1961; Cancino and Von Gadow, 2002). Though more accurate, descriptions of alternative models are often mathematically complex hence do not allow communication between professionals (Ducey, unpublished).

$$y = aq^{n-b} \qquad (4)$$

where: *y*, is the predicted density for a given class; *a*, is the observed density in the highest diameter class; *q*, is a constant; *n*, is the number of classes. *b*, varies for each successive class, with its value being one and *n* in the lowest and highest class respectively.

3.3 Results

3.3.1 *Floristic composition*

Five of the possible nine mangrove tree species found in Kenya were encountered in Mtwapa Creek during the survey: *Avicennia marina, Ceriops tagal, Rhizophora mucronata, Sonneratia alba,* and *Xylocarpus granatum* (Table 3.2). *R. mucronata* occurred as the principal species in all the sites being also the most frequently found with highest density and dominance. *S. alba* and *X. granatum* were only encountered in Gung'ombe and Kitumbo with the former recording low densities in both forest patches (Table 3.2). In terms of dominance, *A. marina* ranked second in all the study sites but with very low densities.

Table 3.2 Structural attributes of Mtwapa Creek mangrove forest: In all the forest patches, *R. mucronata* had the highest values for all attributes.

Forest patch	Species	Height (m)	BA (m²/ha)	Density (Stems/ha)	Relative			IV[a]
					Density	Dominance	Frequency	
Gung'ombe	*A. marina*	7,29 ± 2,37	5.42	88	2.44	37.09	8.70	48.23
	C. tagal	2,20 ± 0,65	0.58	388	10.72	3.95	28.26	42.94
	R. mucronata	3,18 ± 1,02	8.43	3119	86.09	57.65	54.35	**198.09**
	S. alba	5,50 ± 1,00	0.14	12	0.32	0.95	2.17	3.44
	X. granatum	4,50 ± 1,50	0.05	15	0.42	0.36	6.52	7.31
Kitumbo	*A. marina*	7,21 ± 3,56	4.70	169	4.29	27.67	10.14	42.11
	C. tagal	2,65 ± 1,50	1.43	610	15.48	8.45	24.64	48.57
	R. mucronata	3,80 ± 1,20	8.14	2915	73.98	47.99	50.72	**172.69**
	S. alba	5,90 ± 0,95	0.43	51	1.30	2.51	1.45	5.26
	X. granatum	4,30 ± 1,36	2.27	195	4.94	13.38	13.04	31.37
Kidongo	*A. marina*	4,50 ± 3,20	2.54	54	1.86	37.55	14.29	53.69
	C. tagal	2,27 ± 0,84	0.40	438	15.12	5.93	23.81	44.86
	R. mucronata	2,70 ± 0,71	3.82	2408	83.02	56.52	61.90	**201.45**

[a] IV is the ecological importance value of a species. The species with the highest value (**bolded**) is the principal species.

3.3.2 *Vegetation inventory*

Rhizophora mucronata accounted for at least 70% of the total stem density in each of the three forest patches. The other species occurred in mixed formations of *Ceriops-Rhizophora*; *Avicennia-Ceriops*; *Rhizophora-Xylocarpus*; and *Avicennia-Sonneratia*. As a result, there was no distinct separation of vegetation in bands (no clear zonation). *Avicennia marina* showed characteristic large stems close to the water line, but were mostly absent in the landward zone. The other species with major contribution to stem density was *Ceriops tagal*, which however contributed only less than 20% of total stem density in each of the sites (Table 3.3). In Kidongo this species had trees which were frequently stunted.

Table 3.3 Mtwapa Creek mangrove forest stand table. Most poles were of low utilisation class except for *A. marina*. Values in parenthesis indicate percentage proportion of total stem densities.

Forest patch	Species	Utilisation class (butt diametre in cm)^b							Total densty (stems ha^{-1})
		2.5-3.9 (fito)	**4.0-7.4 (pau)**	**7.5-11.4 (boriti)**	**11.5-13.5 (mazio)**	**13.6-20.4 (nguzo)**	**20.5-35.0 (vigingi)**	**>35.0 (mbao)**	
Gung'ombe	*A. marina*	8 (8.7)	4 (4.3)	19 (21.7)	—	8 (8.7)	23 (26.1)	27 30.4)	88 (2.4)
	C. tagal	215 (55.4)	158 (40.6)	15 (3.9)	—	—	—	—	388 (10.7)
	R. mucronata	1265 (40.5)	1473 (47.2)	238 (7.6)	61 (2)	69 (2.2)	12	—	3119 (86.1)
	S. alba	—	—	4 (33.3)	4 (33.3)	4	—	—	12 (0.3)
	X. granatum	4 (25)	8 (50)	4 (25)	—	—	—	—	15 (0.4)
Total stems ha^{-1} by site									**3623**
Kitumbo	*A. marina*	26 (15.2)	44 (25.8)	18 (10.6)	—	36 (21.2)	36 (21.2)	10 (6.1)	169 (4.2)
	C. tagal	200 (33.6)	318 (53.4)	62 (10.3)	10 (1.7)	5 (0.9)	—	—	610 (15.1)
	R. mucronata	1015 (34.8)	1403 (48.1)	364 (12.4)	87 (2.9)	44 (1.5)	3 (0.1)	—	2915 (73.9)
	S. alba	—	13 (25)	31 (60)	3 (5)	5 (10)	—	—	51 (1.3)
	X. garnatum	21 (10.5)	85 (43.4)	46 (23.7)	18 (9.2)	13 (6.6)	5 2.6)	8 (3.9)	195 (4.9)
Total stems ha^{-1} by site									**5831**
Kidongo	*A. marina*	9 (16.7)	7 (13)	—	—	—	20 (37)	18 (33.3)	54 (1.9)
	C. tagal	285 (65.1)	112 (25.5)	41 (9.4)	—	—	—	—	438 (15.1)
	R. mucronata	1392 (58)	938 (39)	69 (2.9)	9 (0.4)	—	—	—	2408 (83)
Total stems ha^{-1} by site									**2900**

b utilization classes grouped according to the Kenyan market and apply Swahili names referring to various uses upon which the poles are put into.

All the species encountered (except for *A. marina* and *S. alba)* had characteristic high stem density that was dominated by diameter size classes ranging from 2.5 to 7.4 cm, suitable for use as *fitos* and *pau*. These low diameter classes, accounted for more than 60% of the total stem densities in all the forest patches. In addition, the stems were mostly of form 3 and thus unsuitable for building (Figure 3.3). Conspicuous absence of utilisation classes with diameter greater than 11.5 cm (in Kidongo) or reduced abundance in Gung'ombe and Kitumbo was also noted.

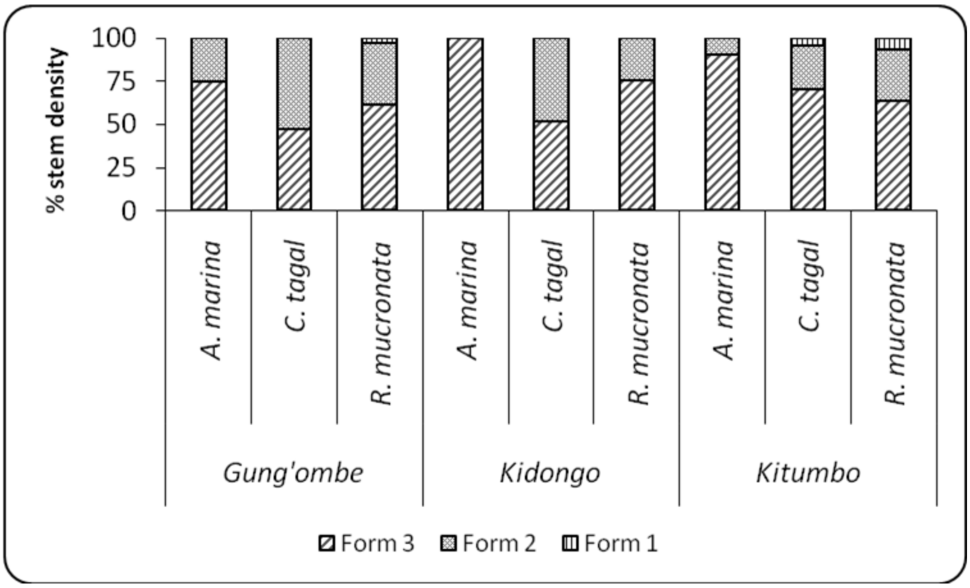


Figure 3.3 Form of lead stems for the three major species found in Mtwapa Creek expressed as a percentage of total stem density. Form 1 are straight and excellent for use in construction, form 2 need slight modification before use and form 3 are completely unsuitable for construction.

Relationship between height and stem diameter of the most dominant species (*R. mucronata)* in the surveyed forest patches is shown in Figure 3.4. All the patches showed similar trends with most trees tending towards an increased height with minimal radial change. However, difference in heights among forest patches and species were highly significant (H =280.9; N= 2365; p<0.01 and H=448.6; N= 2365; p <0.01 respectively). Similarly, differences in stem diameter among forest patches surveyed and between the species encountered were highly significant (H=124.4; N= 2367 p <0.01 and H =178.2; N= 2367; p<0.01, respectively).

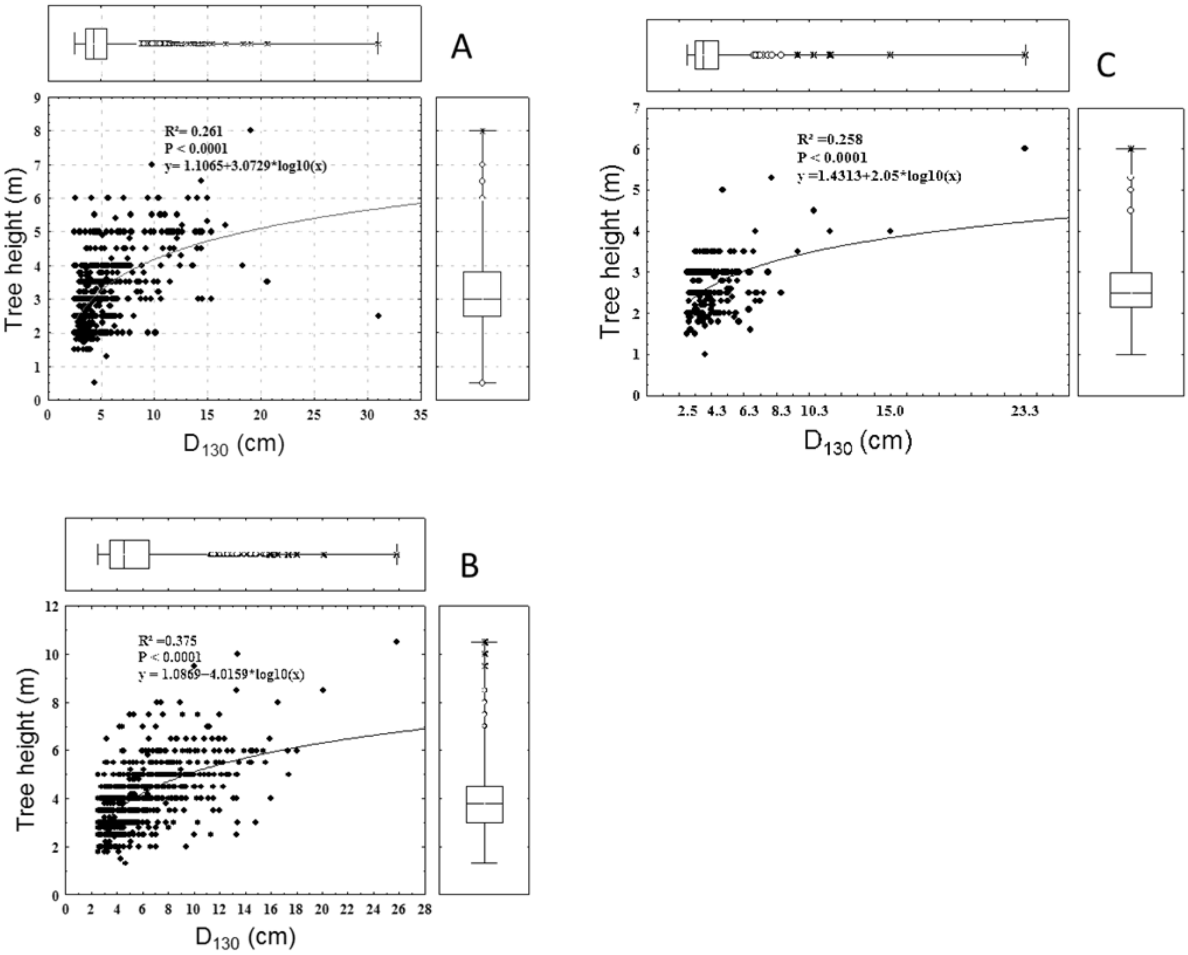
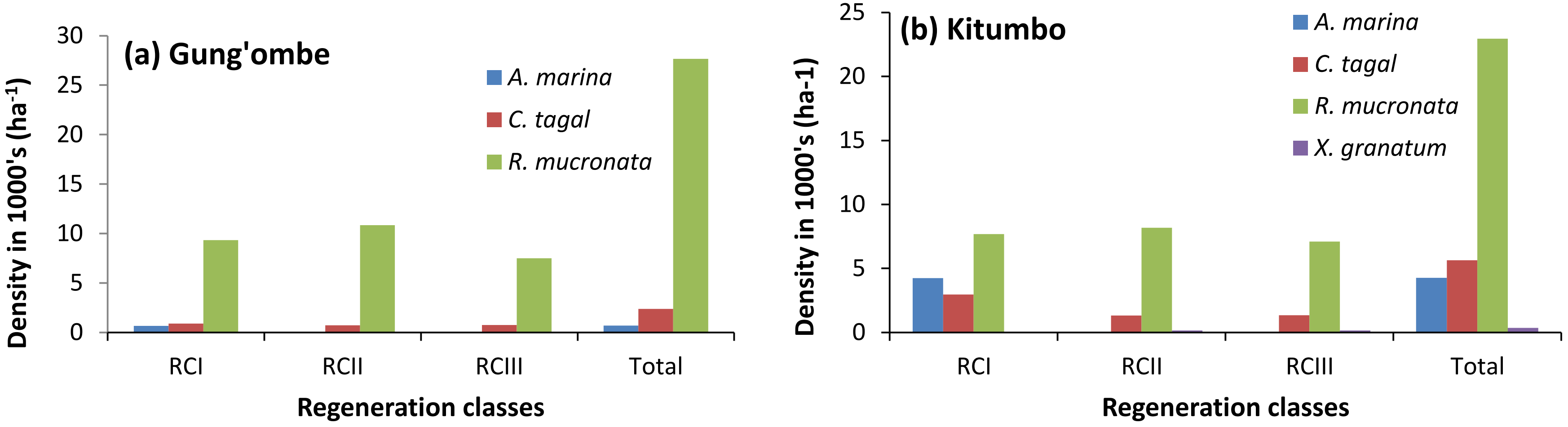


Figure 3.4 Scattergrams of heights against stem diameters of *R. mucronata* in: **A)** Gung'ombe, **B)** Kitumbo and **C)** Kidongo forest patches in Mtwapa Creek. The polynomial equations, correlation coefficients (R^2), and P values are given for all sampling stations. The box plots display percentile distribution with the extremities corresponding to maximum and minimum values in the data set and the ends of box positioned at 25th and 75th percentiles. All the three forest patches have similar trends with most trees tending towards increased height and limited radial growth.

3.3.3 *Regeneration status of the forest*

Large variations were observed in sapling densities, 42 – 27,673 stems ha^{-1} (Figure 3.5a, b and c), depending on species and forest patch. Density of already established saplings (RCII and RCIII) was more or less similar in the three patches; 3302±4681.6, 2280.3±3361.7 and 2882.3±3154.9 stems ha^{-1} (mean±SD) for Gung'ombe, Kitumbo and Kidongo respectively. Major differences were observed across species ($p < 0.05$) in all the regeneration classes. *R. mucronata* saplings accounted for 60% of the total sapling counts in all the forest patches whereas *X. granatum* was observed in very low numbers while no *S. alba* were encountered (Table 3.4). Limited occurrence of *A. marina* was also recorded in which RCI dominated the sapling pool and RCII. Both *R. mucronata* and *C. tagal* had equal distribution of saplings among the regeneration classes indicating possible recruitment success in saplings of the two species (Table 3.5).



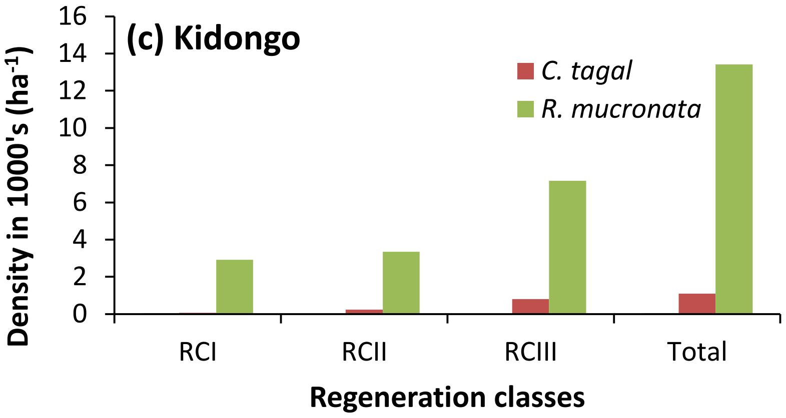


Table 3.4 Sapling ratios of the three major species in Mtwapa Creek mangroves

Site	Tree species	RCI ^{C}	RCII ^{C}	RCIII ^{C}
		<40 cm	40-150 cm	>150 cm
	A. marina	112 (99.2)	0	1 (0.08)
Gung'ombe	*C. tagal*	1 (38.6)	1 (30.5)	1 (31.2)
	R. mucronata	1 (33.7)	1 (39.2)	1 (27.1)
	A. marina	709 (99.8)	0	1 (0.2)
Kitumbo	*C. tagal*	2 (52.7)	1 (23.5)	1 (23.8)
	R. mucronata	1 (33.5)	1 (35.6)	1 (30.9)
	A. marina	42 (100)	0	0
Kidongo	*C. tagal*	1 (5.3)	4 (21.1)	14 (73.7)
	R. mucronata	1 (21.7)	1 (24.9)	2 (53.4)

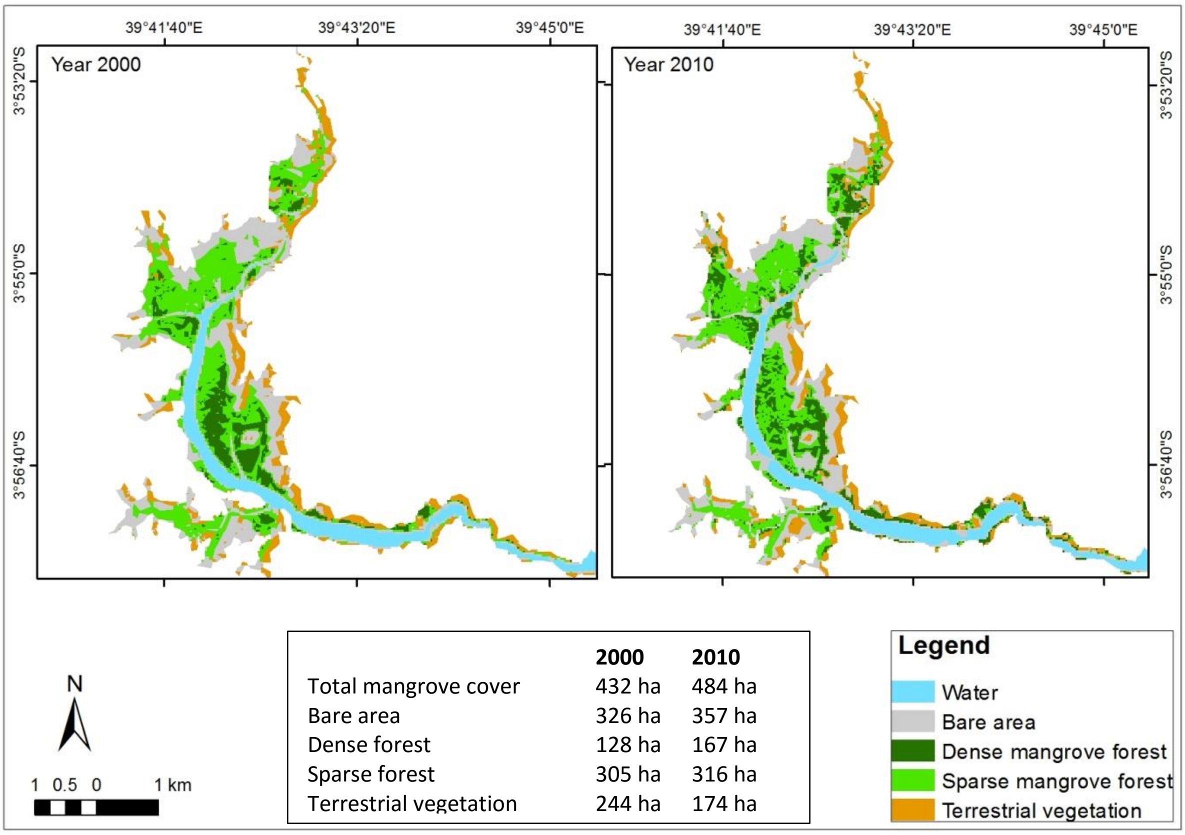
Values in parentheses are percentages of the total stem density per class and species

Figure 3.5 Density of saplings encountered in the three forest patches sampled within Mtwapa Creek mangroves. ^{C}saplings have D_{130} less than 2.5cm and the classes; RCI, RCII and RCIII are grouped according to height

3.3.4 *Vegetation cover and cover change over time*

All the mangrove forest areas surveyed recorded percentage vegetation covers greater than 50%: mean±SD of 70±8, 60±18, 55±14 in Gung'ombe, Kitumbo and Kidongo respectively. Stump density per hectare was higher in Kidongo (2557.1±1000.9) as compared to the Gung'ombe (904±850) and Kitumbo (750±700.2) forest patches. Stumps varied in sizes with large ones being the majority and seemed old. New stumps from recent cuttings were mainly from *paus* (4.0 to 7.4cm) and were only encountered ocassionally (3% of the total stump count). The percentage vegetation cover per quadrat did however not show any significant correlation with the number of stumps ($Z = 1.06$, $p > 0.05$, Mann-Whitney U Test). Further, the relationship between gaps created by cutting (determined from stumps' count), and the number of saplings was not significant ($p > 0.05$) for all the regeneration classes.

For the selected period of cover change analysis, an increase of approximately 51 ha of mangrove was realised mainly within Kitumbo and Kidongo. Certain areas initially covered by sparse mangrove forest had dense vegetation, increasing the dense mangrove areal cover from the 128 ha in 2000 to 167 ha in 2010 (Figure 3.6). Clearing of terrestrial vegetation in close proximity to the mangrove area had seen a reduction in cover from 244 ha in the year 2000 to 174 ha in 2010 resulting in an increase in the bare land category. Due to similarities in reflectance, it was however difficult to separate bare tidal flats from bare dry land in the supralittoral zone. The generated contour map of the area revealed rather steep slopes around the mangrove area as demonstrated by the closely spaced contour lines (Figure 3.7). Slightly further away from the mangrove forest area the terrain appears less steep as compared to the area immediately above the forest.



	2000	2010
Total mangrove cover	432 ha	484 ha
Bare area	326 ha	357 ha
Dense forest	128 ha	167 ha
Sparse forest	305 ha	316 ha
Terrestrial vegetation	244 ha	174 ha

Figure 3.6 Change in mangrove cover in Mtwapa Creek between the years 2000 and 2011

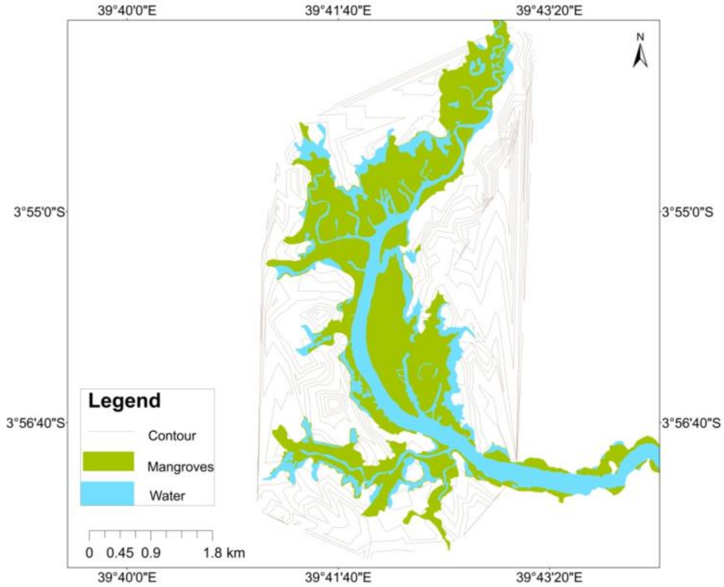


Figure 3.7 Contour map of the area around the mangroves of Mtwapa Creek with the buffer extending 5 – 6 km into the adjacent land. (Contour interval = 100 m)

3.3.5 *Dispersion and population shape of the principal species*

Variation in complexity index among the surveyed sites revealed higher values in Gung'ombe and Kitumbo (12.01 and 15.95 respectively) and a low value of 1.86 at Kidongo. Dispersion according to Morisita index showed a tendency towards uniform distribution for *R. mucronata* adults as well as saplings ($I_\delta < 1$) but a rather clustered pattern ($I_\delta >> 1$) for *C. tagal* (Table 3.5).

Table 3.5 Dispersion indices for the two most abundant adult trees species in the mangrove forest of Mtwapa Creek. Indices >1, the population is clustered; <1, the population is randomly dispersed; and if =1 means the population is evenly dispersed

		Distance from the creek (m)					
Site	**species**	50	100	200	250	300	350
Gung'ombe	*C. tagal*	— (—)	3.0 (—)	1.4 (5.2)	— (—)	— (—)	1.6 (10.3)
	R. mucronata	1.4 (0.9)	1.0 (2.7)	0.9 (0.1)	1.3 (0.1)	1.5 (0.8)	2.57 (2.73)
Kitumbo	*C. tagal*	— (—)	— (—)	0.2 (0.1)	— (—)	0.4 (2.5)	— (—)
	R. mucronata	0.3 (3.3)	1.6 (0.9)	1.2 (1.0)	1.6 (0.4)	1.8 (0.8)	1.0 (4.3)
Kidongo	*C. tagal*	— (—)	1.7 (—)	— (—)	3.0 (7.2)	2.0 (4.2)	1.2 (3.3)
	R. mucronata	1.0 (5.4)	1.1 (0.7)	1.1 (0.7)	1.3 (0.1)	0.1 (0.3)	1.5 (6.9)

The empty entries indicated by hyphens are sampling points where the specific species were absent. Values in parentheses represent saplings.

The principal species showed a deviation from the De Liocourt's balanced diameter distribution with certain utilisation classes (*mazio*, *nguzo* and *vigingi*) completely missing out in Kidongo (Figure 3.8). This absence of classes is an important proxy for determination of selective exploitation of the mangroves by the people.

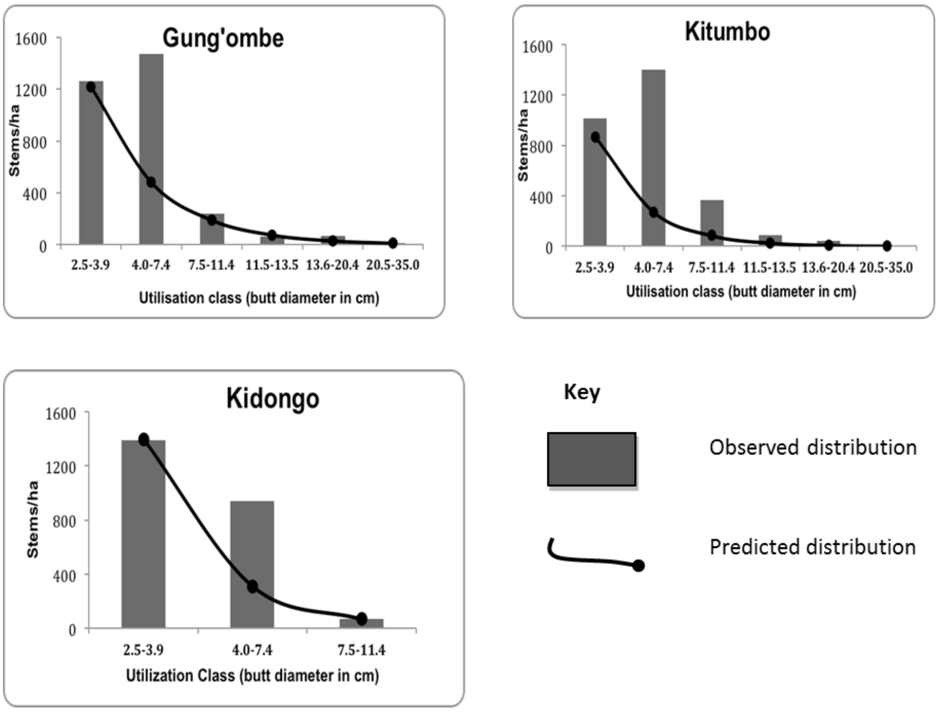


Figure 3.8 Observed and predicted size class distribution of principal species (*R. mucronata*) in Mtwapa Creek, Kenya. Predictions are based on De Liocourt's model (Clutter *et al*., 1983) used to harmonize stand densities from 26, 39 and 13, 10 m by 10 m quadrats sampled in Gung'ombe, Kitumbo and Kidongo respectively. Preferential harvesting of poles is only seen in Kidongo where certain size classes are missing.

3.4 Discussion

3.4.1 *Upper canopy structure*

The structural survey of Mtwapa Creek mangroves realised a relatively low species representation and an indistinct zonation. Such lack of obvious zonation has equally been reported in other mangrove areas in Kenya including Mida Creeks (Kairo *et al*., 2002). In Mtwapa Creek, the phenomenon could as well be attributed to geomorphology as proposed by Snedaker *et al.* (1992) and Bunt and Stieglitz (1999). The narrow tidal flat and steep hills facing the creek (Figure 3.7) limit the landward spread of mangroves species. As a result, the landward *A. marina* zone was frequently absent with the species only occurring as large trees in the seaward zone. Though it is commonly a landward species, *A. marina* may exhibit double zonation in some mangrove forests as has also been reported in Gazi Bay (Dahdouh-Guebas *et al*., 2004a).

The survey established that *R. mucronata* is the principal species in the creek which is a common phenomenon with similar results reported in Mida Creek (Kairo *et al.*, 2002), Tudor Creek (Mohamed *et al*., 2009) and in Gazi Bay (Dahdouh-Guebas *et al*., 2004a). *Rhizophora* spp. can take such a position elsewhere, e.g. *R. mangl*e in Sittee River – Belize (Kangas, 2002) and *R. mucronata* in Sri Lanka (Mangala and Padma, 1998; Karunathilake, 2003). Although *R. mucronata* recorded higher stem densities in Mtwapa Creek (2408-3119 stems ha^{-1}) in comparison to those reported by similar studies in Mida Creek of 433-545 stems ha^{-1} (Kairo *et al.*, 2002) and in Tudor Creek of 750-904 stems ha^{-1} (Mohamed *et al.*, 2009), the equivalent basal area in this study is relatively low. In Sittee River, Kangas (2002) recorded a basal area of 20.8 m² ha^{-1} against a density of 775 stems ha^{-1} for *Rhizophora mangle* (the principal species in that forest). Additionally, even though stem densities of *C. tagal* in this study were more or less comparable to those recorded by similar studies along the Kenyan coast, the basal areas were quite low.

3.4.2 *Natural regeneration as the potential future mature stand*

Natural regeneration observed in the study was highly linked to the standing mature trees composition since the saplings with successful recruitment were majorly from the highly dominant species (Table 3.4). Clustering of saplings of the less abundant species and a uniform dispersion of *R. mucronata* observed is similar to findings by McKee (1995), who attributed variation in densities of new recruits (RCI) of mangroves to distance from reproductive adults. Clustering of saplings may however also be as a result of past cutting pressure.

The observed variability in RCII and RCIII sapling densities could be attributed to factors which affect their survival after the establishment phase (RCI). This may include species' differences in sensitivity to mechanical and physicochemical stress arising from; for example, sedimentation (Terrados *et al.*, 1997; Mohamed *et al.*, 2009), flooding and salinity (Jayatissa *et al.*, 2008), as well as other factors like initial orientation of seedling axis (McKee, 1995). Siltation in Tudor Creek was facilitated by ease of sediment to be carried down the slopes which face the tidal flats (Mohamed *et al.*, 2009). Mtwapa Creek has a similar setting with steep slopes facing the creek (Figure 3.7) and could therefore face a similar problem that might have led to high mortalities of *A. marina* hence low recruitment into successive regeneration classes.

3.4.3 *Implications of structural status of Mtwapa Creek mangrove forest on its sustainability and management*

Spatial analysis of mangrove coverage in Mtwapa Creek reflects an annual increase in coverage of 5 ha between 2000 and 2010 (Figure 3.6). Kirui *et al.* (2012) however recorded a general reduction in mangrove cover in Kenya during the same period though with varying rates across the different mangrove areas, with Kilifi County showing the least loss. Nevertheless, absence of highly preferred pole sizes, *boriti* and *pau* particularly in Kidongo may reflect a higher consumptive extraction of mangrove wood products in close proximity to human settlements (Kairo *et al.*, 2002) as well as ease of access to the forest area. Such selective logging could greatly affect pole quality and the stability of future forest (Kairo, 2001), resulting into a forest with poor form trees composed mainly of stunted and shrubby trees and incomplete representation of utilisation classes (Eusebio *et al.*, 1986; Smith and Berkes, 1993). In addition it may lead to fragmentation and alteration of habitats thus affecting the general stability of an ecosystem (Johns, 1986).

Although selective removal of poles by the cutters (creating small gaps in the forest canopy), stimulates regeneration (Duke, 2001; Kairo *et al.*, 2002) with extremely large gaps inhibiting regeneration (Mohamed *et al.*, 2009), such a relationship was not evident in this study. Natural regeneration was instead found in large numbers which is considered adequate according to FAO (1994) estimations, where such sites have sapling density exceeding 2500 ha^{-1} and the saplings are uniformly distributed as is the case with the principal species in this creek. Against the backdrop of high sapling density the forest appears to develop in to high density with extremely low basal area and poor form in *C. tagal* and *R. mucronata* (the most common species in the study site) trees, suggesting stressful growth conditions in the creek. It could additionally be attributed to history of repeated selective logging which has been demonstrated elsewhere to result in high stem density and associated low basal areas in the affected forests (Smith and Berkes, 1993; Bradley, 2005). Mtwapa Creek mangrove stand also deviates significantly from balanced diameter distribution (Figure 3.8) that is prescribed for sustainability as described by the De Liocourt's model (Clutter *et al.*, 1983). Currently, no licences are issued for mangrove cutters in the creek but when they were, the management regime concentrated solely on quantity harvested by placing and lifting bans randomly without an established mechanism to ensure sufficient turn over (Bosire and Kairo, 2008; Government of Kenya, 2009). As a result, the management has failed to take note of cryptic ecological degradation and ensure sustainability.

Human activities in the riparian zone and catchment areas could also impact on self-sustenance potential of the forest. For instance, a land use land use change (LULC) study by Bosire *et al*. (2015) around Mtwapa Creek shows a considerable reduction in terrestrial forest land between the years 1990 and 2009 from 3357 ha to 899 ha and an increase in agricultural land (838 ha to 3052 ha). This coupled with the hilly terrain around the mangroves area (Figure 3.7) could increase sedimentation in adjacent mangroves with terrigenous sediment and its impacts on tree growth cannot be downplayed. High sedimentation rates (greater than 1cm a year) may lead to stress, dieback and even death (Ellison, 1998). In the adjacent mangrove forest of Tudor Creek (with a similar setting), sedimentation was found to impact negatively on seedling development (Mohamed *et al.*, 2009). In Mwache Creek situated South of Mtwapa Creek, poor land use practices in the hinterland have increased sediment loads into the mangrove forest leading to burial of breathing roots of the trees and eventual death of the trees (Kitheka *et al.*, 2002).

3.5 Conclusion

The results of this study showed that there was an increase in mangrove forest cover within the 10 year period before the survey but this may not necessarily negate overexploitation in Mtwapa Creek. Instead it suggests recovery which is underscored by the observed high natural regeneration. This mangrove forest has sufficient natural regeneration but poor tree development thus hindering the forest's self-sustenance. Apart from geomorphology which influences the extent of landward spread of mangroves, selective logging particularly in Kidongo has been noted to impact negatively on the integrity of the forest. Other stress causing forms of disturbances could as well be limiting tree development in Mtwapa Creek. With the steep slopes facing the mangroves and the LULC reported from other studies, potential of sedimentation cannot be overlooked.

CHAPTER 4:

State and future of mangroves of Mtwapa Creek -Kenya as perceived by the local communities

Manuscript ready for submission

Abstract

Background: Dependence of village communities on mangroves may be substantial. As a result, mangrove ecosystems have suffered degradation as they are overexploited to serve the ever increasing demand for fuelwood, building poles among other wood and wood products. Exploitation is in addition to the human activities along the riparian areas which may also have considerable influence on adjacent mangrove wetlands. These include but are not limited to, agriculture, industrial production and urbanisation.

Objectives and methods: Socioeconomic characteristics of five local communities living around Mtwapa Creek were examined to establish their perceptions on the status of the adjacent mangrove forest.

Results: The main economic activity practised by the communities living near the mangroves in Mtwapa Creek is farming with most farms located in close proximity to the creek. Although local communities distant themselves from responsibility on the status of the forest which they perceived as being poor, they appreciated mangroves as an integral component of their livelihood. Mangroves were valued mainly as a source of building and construction material particularly by the male respondents while women mentioned fuelwood. The respondents believe that the mangrove status of Mtwapa Creek has been poor characterised by lack of poles suitable for construction since the past and that the situation has either remained the same or has in fact worsened.

Conclusion: The results bring out mixed opinions amongst local coastal communities on the past, current and expected future status of the mangrove forest. The results show that the difference in perception is associated with their gender, living standards, education level and knowledge about mangrove as a resource.

Contributors: Okello J.A.- main author; Alati V.M.,.- data collection & write-up; Choge S. - mapping & write-up; Kairo J.- supervision; Dahdouh-Guebas- study design & supervision; Koedam N.- lead promoter, study design and supervision.

4.1 Introduction

Mangroves provide both locally and above the local scale products and services, but local communities may have the closest relation to mangroves through their livelihood and direct impacts. Hence, the perception of both utilization and impact are intimately related. The basis of local livelihood and mangroves may include timber and non-timber forest products such as building materials, firewood, tannin, fodder and herbal medicines (Dahdouh-Guebas *et al.*, 2000; Balmford *et al.*, 2002) . Mangrove ecosystems also serve as important breeding and feeding grounds for many species of fish, mollusks, crustaceans and birds (Saenger, 2002; Crona and Rönnbäck, 2005; Lee *et al.*, 2014) which can be harvested by local communities within the mangroves or adjacent systems. Depending on the quality of the forest, mangroves are considered to prevent coastal erosion and play a crucial role in mitigating disaster risk by acting as barriers that dissipate wave energy (Dahdouh-Guebas *et al.*, 2005b; FAO, 2007a; Lee *et al.*, 2014). The arguments by these authors align with those of Das and Vincent (2009) who unlike the others, used data on several hundred villages to prove that mangroves would indeed protect lives from incidences of cyclones and tropical storm surges. Mangroves also help in sediment stabilization through their active growth and deposition of organic matter (Tonneijck *et al.*, 2013) and mitigation of climate change impacts can be expected from their high carbon storage capacities (Donato *et al.*, 2011).

Owing to the multiple benefits that accrue from mangrove ecosystems, establishing a balance between the extractible and non-extractible gains remains a challenge (Millennium Ecosystem Assessment, 2005; Okello *et al.*, 2012), as the benefits are also not tuned to accrue at the same time scale and not to the same people. In fact while making important steps towards achieving the vision 2030, Kenya for instance has still been encountering challenges in reversing environmental degradation (Government of Kenya, 2007). As a result, mangroves have faced continued cover loss in Kenya (Kirui *et al.*, 2012) as well as globally (Duke *et al.*, 2007; Spalding *et al.*, 2010). The progressive rise in population along coastal areas (McGranahan *et al.*, 2007; Samoilys *et al.*, 2015), and the consequent increasing demand for agricultural land, urban development as well as other forms of related anthropogenic disturbances have subjected mangroves to increased pressure. and degradation (Bosire *et al.*, 2013). Land use practices including poor farming practices particularly in the riparian and catchment areas, damming of rivers, clearing of vegetated areas for development and poor location of properties tend to increase instability of physical coastal formations and hence increased soil erosion and consequently degradation of mangroves (UNEP, 2001).

Moreover, Mukherjee *et al.* (2014) on basis of expert views indicate that degradation due to development may require the longest time to restore mangrove functionality as opposed to other forms of degradation.

Several attempts have been made worldwide and in Kenya to restore degraded mangrove areas (Field, 1996; Kairo *et al.*, 2001; Okello *et al.*, 2012) and to ensure effective management of these forests. It is in fact appreciated that conservation and sustainable management is a superior strategy to restoration or reforestation (Vannucci, 2004). Mangroves in Kenya were legally declared as government reserve forests since the Proclamation No. 44 of 30th April 1932, and later by Legal Notice No. 174 of 20th May 1964 (FAO, 2007b). The management of mangrove forests began in 1951 when the colonial government introduced the first Mangrove Working Plans for Lamu. Unfortunately it has been limited to the licensing of extraction of wood products, authorized by the Ministry of Environment and Natural Resources; annual quotas for extraction are decided on unspecified basis, and extractions operations are not always supervised (FAO, 2007b). However, the new forest Act No. 7 of 2005 now provides for involvement of the private sector and local people in mangrove management through the formation of Community Forest Associations (CFAs) (Samoilys *et al.*, 2015). This system is quickly picking pace along the coast and could offer a breakthrough (Frank, 2014). Further, the assumption that people always destroy mangroves has been put to question following the self-initiated mangrove planting and management programs by the local people (Walters *et al.*, 2008)

Socio-economic studies have been conducted among various communities living adjacent to mangrove forest patches in Kenya to analyse utilisation pattern and establish possible cause-effect relationships between the people and these forests (Kairo, 1992; Dahdouh-Guebas *et al.*, 2000; Mohamed, 2008). However, since demographic characteristics of local human communities may vary significantly from one geographic locality to the other (Government of Kenya, 2012), each mangrove area has to be treated as a separate entity for purposes of effective integration into national management plans. It is also important to incorporate local perceptions in order to ensure successful conservation ventures of natural resources (Nazarea *et al.*, 1998; Horowitz, 2001; Marcus, 2001; Frank, 2014).

This section of the study highlights the nature of activities of the local human community and the impacts they may exert on the bordering peri-urban mangrove ecosystems. This was achieved through analysis of the perception of the respondents against a background of their socio-economic characteristics and secondary data on mangrove harvest. Such understanding of how socioeconomic characteristic influence people’s values of the environment can be an important tool in the development of an effective conservation strategy while solving the real causes of degradation of a resource (Cinner and Pollnac, 2004). The underlying hypothesis was that socioeconomic status (village, education, income, gender, house type) is associated with the nature of activities by local communities, with impacts they may exert on the adjacent mangrove ecosystem and their perceptions on the status of this resource.

4.2 Materials and Methods

4.2.1 *Study site*

The study was conducted in five villages along Mtwapa Creek, Kenya (3° 57' 0 S, 39° 45' 0 E), bordering Mombasa and Kilifi counties to the South and North respectively (Figure 4.1). The general settings are described in section 1b.2. The villages (Kashani, Kidutani, Mdengerekeni, Mtepeni and Mtomondoni) which border the creek from both shores were chosen purposively based on proximity to the mangrove forest (Figure 4.1).

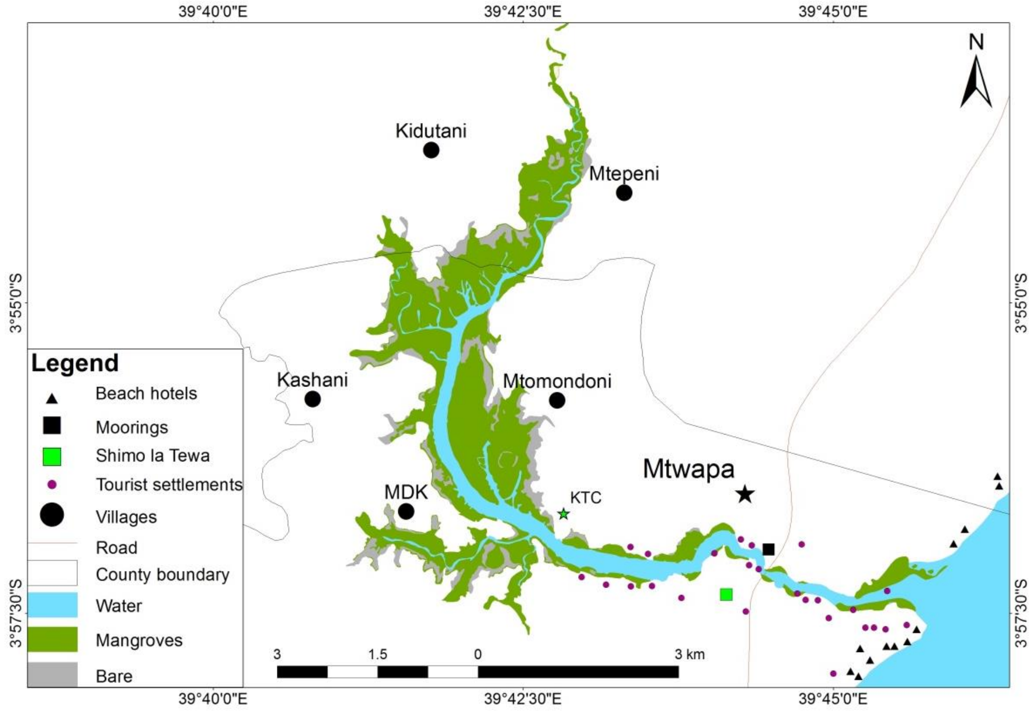


Figure 4.1 Map of Mtwapa Creek showing the location of the five villages, Mtomondoni, Mtepeni, Kashani and Mdengerekeni (MDK), within which the interviews and focus group discussions were conducted. Kwetu Training Center (KTC) and several hotels and touristic settlements are also shown as well as the Shimo la Tewa prison. Source: Kenya Marine and Fisheries Research Institute database.

As per the Kenya electoral boundary commission, the surveyed villages fall under two sub-locations, Shimo la Tewa and Mtepeni (Government of Kenya, 2012) which have a population density of 21 and 65 persons per km^2 respectively (Government of Kenya, 2010). As per data obtained from the village heads, Kashani, Kidutani, Mdengerekeni, Mtepeni and Mtomondoni villages have 142, 258, 92, 284 and 308 households respectively.

Current laws ban individuals from cutting mangroves but licences are offered to mangrove cutters most of whom do not live around the study area. With the supervision of Kenya Forest Service (KFS), such individuals are expected to cut within a given locality. In Mtwapa Creek, no licences are issued anymore for cutting. Upon the placement of presidential ban on local harvesting of mangroves in the year 2000 (Abuodha and Kairo, 2001), the local community are only allowed to collect dead wood for use as firewood upon being issued with permits by KFS. Such permits costs about half a dollar per week and a bundle of firewood (*tita*) is sold for USD 1.19–1.78 (exchange rate 1 = KES 84, in 2011).

4.2.2 *Methods*

Primary data was collected in April 2011 to gain insights on the socioeconomic characteristics of the local communities and their perceptions of the status of the mangrove forest of Mtwapa Creek. This was achieved through a combination of techniques including; participant observation, photographs, transect walks, semi structured interviews, key informant interviews, and focus group discussions (Bunce *et al.*, 2000). Kiswahili was the general language used in communication and where necessary, the local language was integrated in to the conversations to enhance understanding since the indigenous inhabitants were from the native Mijikenda community. The questions were administered by Okello, Mwakha and the Kenya Marine and Fisheries Research Institute (KMFRI) socio-economic team (see acknowledgement) with assistance from one member of the local community identified by each village head and who could identify well with the people and speak the local language fluently. The following section details the data collection methods that were applied.

Participant observations - where the data collection crew got involved in the activities of study- were useful for the better understanding of activities and as a way to bond with the respondents, hence obtain insight into what the activities meant to them. Transect walks and photographs were mainly employed to capture activities and features of specific interest.

Semi-structured interviews were administered randomly to selected households from a full list of households in the five villages provided by the village heads. Selection of households was done by the team without influence from the village heads to avoid bias. In case all persons from a selected household were absent during the survey, the next home in the row would be visited. Only one member per household (in most cases the household head) was interviewed with exception of where another member contributed significantly to the family earnings. A total of 17, 31, 11, 34 and 37 persons, making up 12% of the total number households provided by the village heads, were interviewed in Kashani, Kidutani, Mdengerekeni, Mtepeni and Mtomondoni respectively. These individuals were from 122 households in the villages. The questionnaires containing both open and closed ended questions were applied. This way, it was possible to probe answers, follow up questions as they appear in the questionnaires and pursue new ideas. The questions explored their demographic and socio-economic characteristics; harvesting techniques of mangrove-related products for various uses; and their perceptions on the state mangroves as well as land-based activities they were engaged in (Annex IIIa).

Key informant interviews provided qualitative data that were used for cross-validation of the results obtained from the questionnaires. The key informants were selected through prior communication with the village heads in order to gain confidence of the individuals. This is because mangrove harvesting is considered a sensitive issue and local communities tend to shy away from discussing it. The village heads together with the key informant also helped identify participants for focus group discussions in each village. Willingness to be interviewed was the overriding factor for one to join the discussion group. Other factors such as gender balance and main economic activities of the respondents were used as secondary criterion. One focus group discussion was conducted in each of the five villages. Each focal group had a 5-10 members with whom a series of open ended questions were discussed.

Questions regarding knowledge were gauged as follows:

- Good working knowledge: Interviewee is able to explain what mangroves are, to identify at least three common species, to identify at least three uses of mangroves
- Rough idea: Interviewee can associate mangroves with the intertidal area but does not know species. He/she knows the main use of mangroves in the area
- No idea: Interviewee does not know anything related to mangroves

Secondary data on mangrove utilisation in Kilifi County was obtained from the draft national mangrove management plan (NMMP, under preparation). The data available was between the year 1990 and 2012. Additional information was provided by Kenya Forest services (KFS) and municipal council of Mtwapa town.

4.2.3 *Data analysis*

Data analysis was done using Ms Excel table sheets and SPSS 17.0 software. The analyses employed were majorly descriptive, which help to transform raw data into a form that summarizes a set of factors in a way that is easy to understand and interpret. Various quantitative variables in the study were also tested for relationships. The data sets by village did not meet the requirement of parametric test even after being transformed. Kruskal-Wallis indicated that there was no statistically significant differences in age of respondents between the villages visited ($H(4) = 3.287$, $p = 0.511$). In subsequent statistical tests, the villages were thus considered as one entity when dealing with age as a factor. Association among various variables was tested using the Pearson Chi-square.

The presence or absence of 18 material of life indicators which are regarded as measures of the wealth of households were recorded in each case (with guidance from the key informants). These comprised of: mode of house construction including house type (permanent, semi-permanent, temporary); roof type (coconut fronds-*makuti*, other leaves, iron sheets or tiles); wall type (*makuti*/other leaves, poles and mud, stones/bricks, other); cooking fuel (fuelwood, charcoal, kerosene, other) and lighting fuel (kerosene, candle, electricity, other). Of the 18 items, only 5 (semi-permanent house, temporary house, iron sheet roof, *makuti* roof, sticks-and-mud wall) which were common across the five villages and were not owned/ used by all respondents were factor analysed using principal component analysis (Cinner and Pollnac, 2004). The items with the highest positive loadings have a stronger contribution on wealth than those with low or negative loadings (Cinner and Pollnac, 2004). Wealth in turn significantly influences how people perceive coastal resources. For instance, wealthier individuals have a greater understanding of indirect causes of degradation of these resources (Cinner and Pollnac, 2004).

4.3 Results

4.3.1 *Socio-economic profile of the respondents around Mtwapa Creek*

The overall sex ratio of the respondents was 6:4 for the male against female. However, there were variations among the villages surveyed (Table 4.1). No official population data for the villages visited could be obtained for this study but the general statistics and population growth around Mtwapa Creek is given as per 2009 census. The primary data collected showed an overall mean household size of seven members with Mtepeni village having significantly higher frequencies of large household sizes (F=4.066, $p<0.05$) than the rest of the villages. Ninety-four (94) % of all the respondents were household heads while the rest were dependants who lived with their parents or guardians but contribute in one way or the other to the household's income (Table 4.1).

Education levels were quite low among the respondents. On average, most of the respondents had primary level education (48.8%), with the least proportion attaining secondary education (7.9%) and the remainder respondents had no formal education.

Table 4.1 Description, mean and variation of the respondents living in the 5 villages surveyed around Mtwapa Creek. Only two of the respondents from Mdengerekeni were not natives of the area while the rest were all Mijikenda.

Indicator	Description	Villages	Range (mean ± standard deviation)
Age	Age of respondents	Kashani	20 – 59 (38.0 ± 12.4)
		Kidutani	18 – 80 (46.2 ± 19.2)
		Mdengerekeni	23 – 66 (45.5 ± 13.4)
		Mtepeni	18 – 70 (43.6 ± 15.5)
		Mtomondoni	19 – 85 (47.2 ± 17.5)
		Total	18 – 85 (44.7 ± 16.6)
Gender	Percentage number of respondents of a given sex	Kashani	Male 76.5%; Female 23.5%
		Kidutani	Male 61.3%; Female 38.7%
		Mdengerekeni	Male 90.9%; Female 9.1%
		Mtepeni	Male 41.2%; Female 58.8%
		Mtomondoni	Male 48.6%; Female 51.4%
		Total	Male 41.2% – 90.9% (63.7 ± 20.4%)
			Female 9% – 59% (36.3 ± 19.2%)
Household size	Number of individuals per household including dependants both children (< 18 years old) & adults (>18 years old)	Kashani	1 – 10 (3 ± 3)
		Kidutani	2 – 15 (7 ± 4)
		Mdengerekeni	2 – 11 (6 ± 3)
		Mtepeni	4 – 24 (8 ± 4)
		Mtomondoni	1 – 21 (7 ± 4)
			Total 1 – 24 (7 ± 4)
Income	Percentage number of respondents with selected income ranges earned per week (1 US$ = KES 84)		US$ 0 – 5.95 10% – 46% (31 ± 13.2%)
			US$ 5.96 – 11.90 11% – 40% (26 ± 11.1%)
			US$ 11.92 – 17.86 9% – 40% (18 ± 12.4%)
			US$ 17.87 – 35.71 8% – 32% (19 ± 10.7%)
			US$ >35.71 0% – 16% (6 ± 7%)

---

1 USD was equal to EUR 0.904 as at the time the study was conducted.

4.3.2 *Livelihoods in Mtwapa Creek local communities*

Most respondents (31%) reported an average annual income of less than USD 285.6 (EUR 258.2) per year (Table 4.1). This value also includes goods for direct consumption produced by each household.

Farming provided the major source of income in the area contributing more than 60% of the total revenue. A total of 49.6% of the respondents practised farming (Figure 4.2) and 67% of these farmers were engaged in farming activities as a full time activity while the rest do it as a part time. Casual labour and trading in small scale businesses involving fast moving household goods (mainly food stuffs) was considered the second and third most important source of livelihood respectively by local communities in Mtwapa Creek (Figure 4.2). Those living in Mtomondoni and Kidutani villages depended more on trading while those from Kashani and Mdengerekeni were mainly casual laborers in building and construction industries and in agricultural farms. Those who were employed on either permanent or contract basis worked in the beach hotels, or as teachers in schools and in various industries in Mombasa city and Mtwapa town. There was however no form of relationship established by the study between location of villages with respect to the two major towns and the people's engagement in employment.

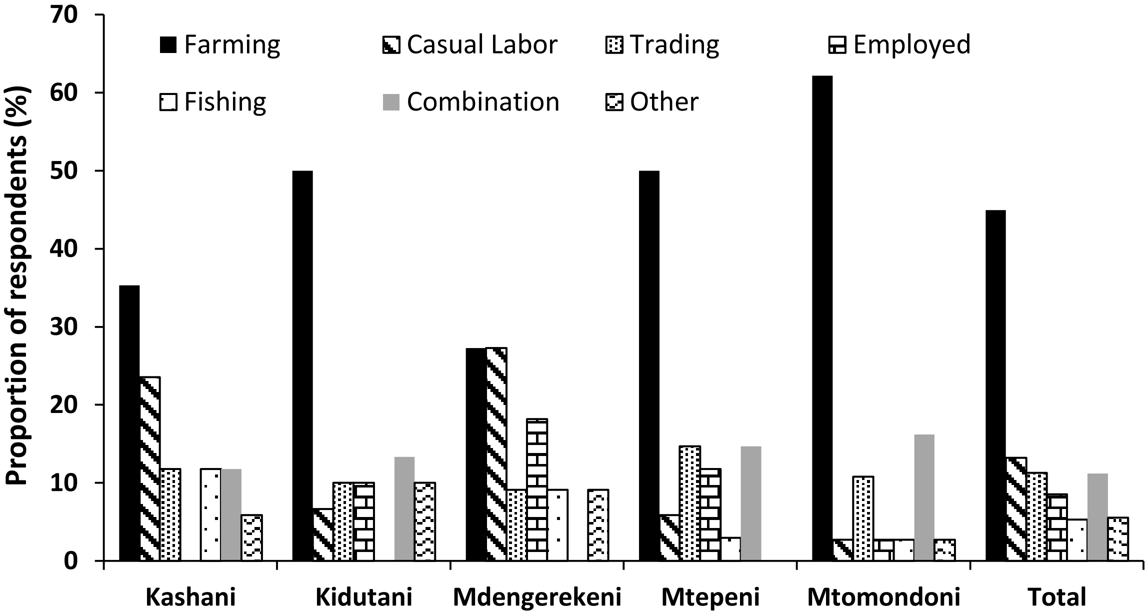


Figure 4.2 Economic activities of the people living in the five villages surveyed around Mtwapa Creek

Other important income generating activities that the respondents were engaged in included: fishing and masonry. Although fishing was considered important, it only accounted for 3.9% of local community income sources as it is practised by a small proportion of people living close to the creek mainly in Kashani and the adjacent villages of Kidongo and Majaoni. The fishing is artisanal, undertaken for both subsistence and commercial needs. The fishermen use small traditional fishing boats and cast nets or employ hook and line fishing. Fish catch seldom reach the nearby Mtwapa town as it is often sold at the landing site directly to the local communities or to local fish traders who supply fish within the same villages.

From the focus group discussions, it emerged that both farming and fishing have had their fair share of dwindling returns over the years. Fish catches were reported to have progressively declined attributed to reduction in depth of the creek. The reduction of depth was said to be as a result of sediment deposition in the creek water ways but the local fishermen were not able to systematically ascertain the sediment source. Farming on the other hand had been affected by bad weather conditions and escalating cost of farm inputs forcing men to seek employment as casual labourers in the fast expanding town of Mtwapa and Mombasa city while women engage in small scale businesses such as sale of food stuffs. The conspicuously low level of education (more than 40% having no formal education) greatly affected the level of engagement in formal employment considering that more than 70% employed had some education (Figure 4.3). From the interviews, it was clear that the fluctuations in trends of engagement in various activities always followed a rising opportunity and the need for better earnings.

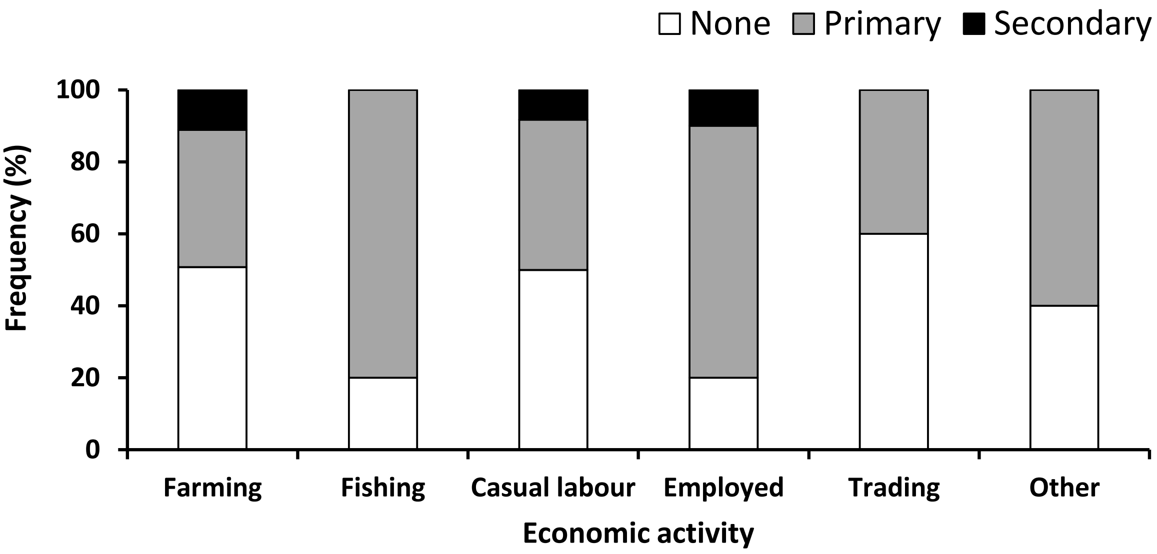


Figure 4.3 Local community's engagement in various economic activities as a function of education level of the respondents.

4.3.3 *Material style of life of local communities adjacent to Mtwapa Creek*

The study established that most of the houses, 68.8%, were made of temporary structures, with semi-permanent and permanent houses constituting only 25% and 6.2% of the total sample respectively. A cross tabulation of mangrove usage against house type revealed a significant association between the two (χ^2 (3, N= 130) =8.74, $p<0.05$).

Compared to the other villages in the study, Mtomondoni had the highest proportion of items perceived to be owned by the more privileged in the society followed by Mtepeni (Table 4.2a). These include permanent houses, iron sheet roofing, stones/ brick walls and electricity lighting (Pollnac and Crawford, 2000). Results from factor analysis of the 5 selected indicators showed that they all had high factor loading in the five villages except sticks-and-mud wall in Kidutani and Mdengerekeni (Table 4.2b). The extraction showed one component that explained more than 70% of the variance in each of the villages.

Table 4.2a Percent number of individuals associated with a given material style of life items in the five villages surveyed in Mtwapa Creek. The percentages for each item is compared across the 5 villages

Items	Villages				
	Kashani	Kidutani	Mdengerekeni	Mtepeni	Mtomondoni
Permanent house	0	0	0	12	88
Semi-permanent house	16	22	6	31	25
Temporary house	12	27	10	26	25
Iron sheet roof	13	20	4	27	36
Makuti roof	13	26	9	26	26
Other leaves as roof	0	33	67	0	0
Makuti wall	0	0	100	0	0
Sticks-and-mud wall	13	28	8	27	24
Stones/bricks wall	17	0	0	18	65
Other wall type	0	0	0	100	0
Charcoal cooking fuel	0	0	0	0	100
Firewood cooking fuel	12	25	9	27	27
Kerosene cooking fuel	100	0	0	0	0
Other cooking fuel types	0	0	0	0	100
Candle for lighting	83	0	0	17	0
Electricity lighting	0	0	0	0	100
Kerosene lighting	9	25	10	29	27
Other lighting sources	20	0	0	0	80

Bold denotes common items across the villages; italicised are items present in/ used by all households

Table 4.2b Principal component analysis of selected material style of life found in the villages surveyed

Items	Villages				
	Kashani	Kidutani	Mdengerekeni	Mtepeni	Mtomondoni
Semi-permanent house	**-0.933**	**0.957**	**0.989**	**-0.924**	**-0.741**
Temporary house	**0.906**	**-0.957**	**-0.989**	**0.976**	**0.956**
Iron sheet roof	**-0.971**	**0.953**	**0.989**	**-0.97**	**-0.954**
Makuti roof	**0.971**	**-0.92**	**-0.725**	**0.937**	**0.954**
Sticks–and-mud wall	**0.758**	0.159	0.224	**0.668**	**0.887**
% of variance explained	83.027	72.198	70.16	81.398	81.422

Bold denotes high factor loading (> 0.4)

Households depended mainly on wood for cooking with more than 90% of the respondents using firewood in all the villages. Fuelwood collection was done by women who did not wish to reveal the source of the wood. There were however no woodlots observed in the area during the survey. In addition, the results from the interviews revealed that villages which are much closer to the mangrove patches and where the terrain allowed ease of access (Kidutani, Mtomondoni and Mtepeni) had 100% dependency on firewood. These are villages within a range of 2 km from the creek. Alternative sources of energy mentioned by the respondents were kerosene, palm fronds and gas.

4.3.4 *Mangrove goods*

The local community had varying levels of knowledge on the importance of mangroves either imparted to them by Kwetu training centre, a non-governmental organisation (NGO) situated along the creek (Figure 4.1), or simply through personal experience. Kwetu training centre also offers trainings on alternative livelihood option and offers financial support to community groups willing to engage in such ventures. A large percentage of those interviewed had a good working knowledge (61.8%), while 33.3% had a rough idea and only 4.9% had no idea about the role of mangroves. The results showed no association between age category and knowledge level (χ^2 (8, N=125) =3.6, p>0.05). However, there was a significant association between education level and knowledge on mangroves (χ^2 (9, N=130) =48.96, p<0.001). Examination of frequencies showed that of the 61.8% of those interviewed with good working knowledge, 92% either had no education or only primary level (Figure 4.4). Though the number of non-native individuals (not of coastal origin) encountered was too small to make a conclusive remark, the two both engaged in trading and farming and had no idea of what mangroves are.

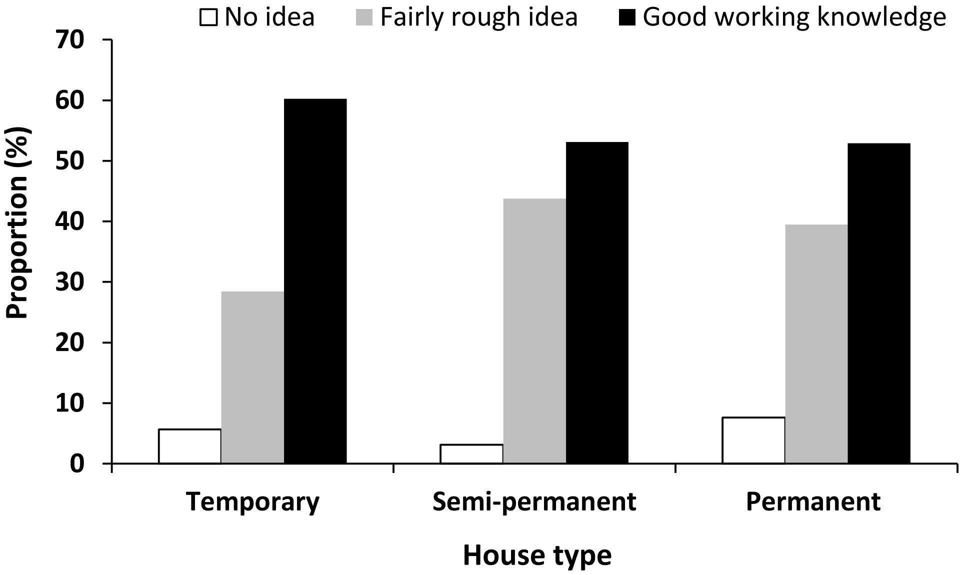


Figure 4.4: Knowledge of the local community on mangroves in relation to the respondent’s house type**.**

Of the known mangrove importance, construction was the most mentioned in all the five villages (Figure 4.5a). More men than women considered construction as the most important mangrove use while fuel wood was preferred among women (Figure 4.5b). Additionally, our observations showed that more households in temporary houses made most use of mangrove goods in each of the categories identified.

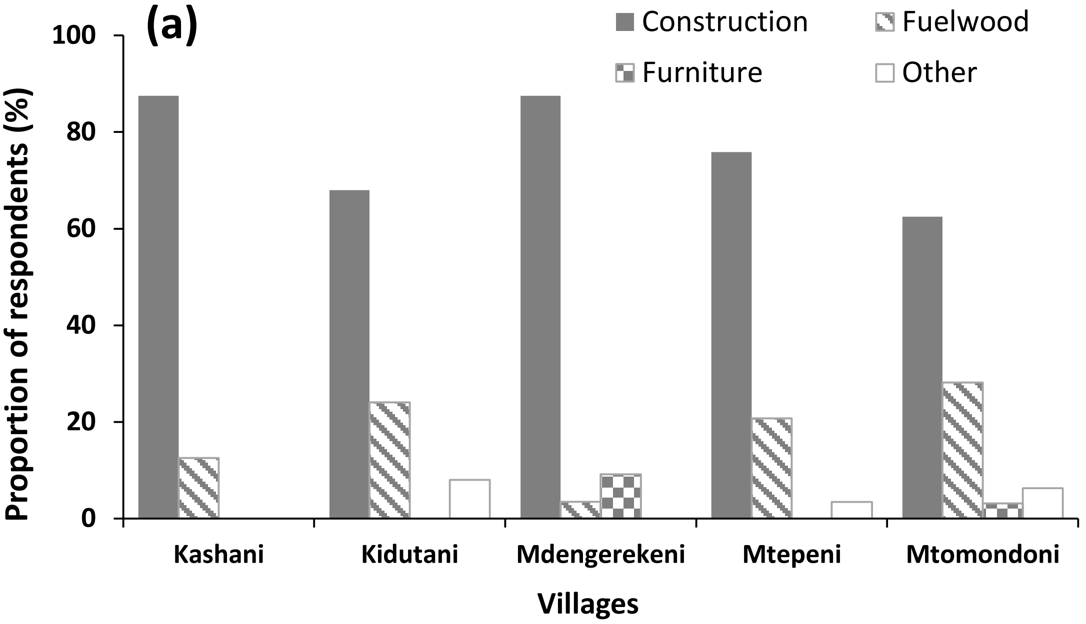


Figure 4.5 (a) Mangrove usage patterns in the five villages surveyed around Mtwapa Creek

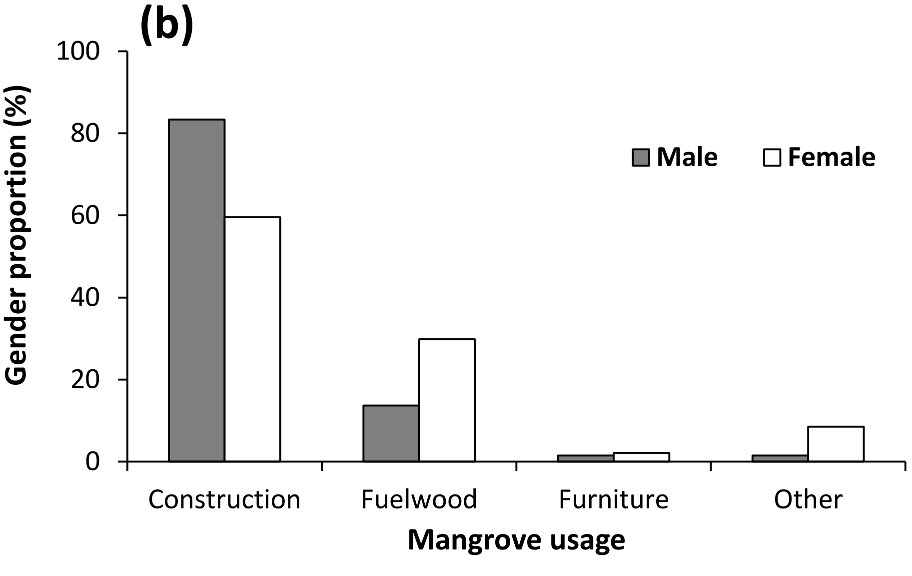


Figure 4.5 (b) Preferred mangrove usage grouped by gender of the respondents

Preference in usage of mangrove products did not only vary by gender but also by age as was established from the key informant interviews. Children engaged in simple fishing activities where they catch crabs and small fish within the tidal inlets during low tide, while the adult males mostly referred to mangrove forests as a source of building materials. Other uses that were considered important locally were mangroves as fencing poles, charcoal, mariculture grounds, medicinal herbs and ecotourism.

Eighty-six (86)% of the respondents admitted that mangroves are exploited in Kilifi County, but of these, only 41% said mangroves in Mtwapa Creek are harvested. Cutting of mangrove trees for construction of houses was mentioned in all the villages. Harvesting of standing mangrove trees for charcoal production in Mtepeni was also mentioned by respondents from Mtomondoni village. Most of the charcoal was not used locally but transported by both middlemen/ self out of the area for sale in the nearby Mtwapa town at 2 km and Mombasa at 15 km by road. Secondary data on mangrove harvesting revealed that illegal harvesting is a major threat for the mangroves in Kilifi County (Figure 4.6). Losses due to illegal harvesting of construction poles and fuelwood progressively increased after the imposition of total ban on harvesting of mangrove wood in the year 2000 (Figure 4.6c and d). It should be noted that the harvest data is for the entire Kilifi County and may only partly reflect the harvest in Mtwapa Creek.

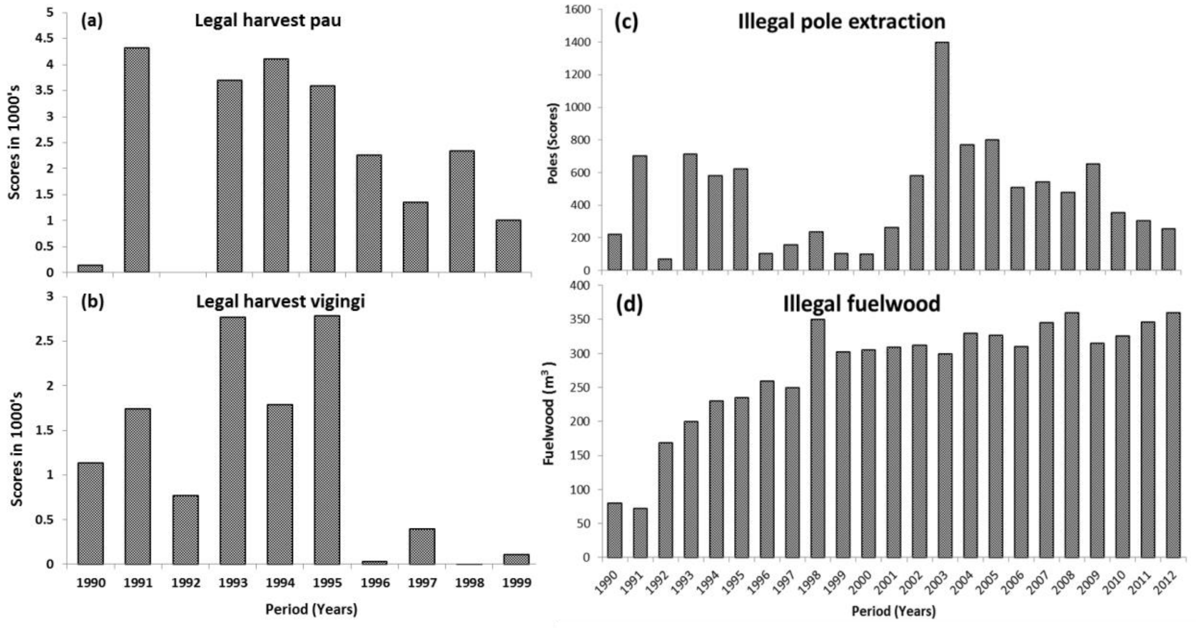


Figure 4.6 Legal (a, b) and illegal (c, d) Mangrove wood extraction in Kilifi county. Only pau (butt diameter 4.0 – 7.4 cm) and vigingi (20 – 35 cm) were allowed to be harvested before the ban in the year 2000. Data obtained from KFS and the National Mangrove Management Plan (NMMP) working group

Local communities are well aware of restricted access to the resource, most of the harvesting in Mtwapa Creek occurs in the heart of the forest as this prevents the trespassers from being sighted by the forest guards. The trend was similar in the five villages with no significant association noted in the response obtained from either various age groups or education status. Local respondents blamed illegal harvesting on the high poverty levels in the area, laxity of KFS guards and corruption. Overall in Kilifi County, a complete ban was placed in the year 2000 to 2005, a period which saw a significant rise in estimated illegal extraction of mangrove poles from 348.5 scores[▲] to 650 scores annually and firewood from 214.8 m^3 to 313.8 m^3 annually (Appendix I Table S2- data from KFS).

4.3.5 *Perception of forest status and causes of degradation*

Fifty-three percent (53%) of the respondents said that the forest was depleted of poles that could be used for construction. A total of 38% of the respondents stated that the forest status was good or recovering while another 9% felt it is very healthy. There was a significant association between gender and response on forest status (χ^2 (5, N= 100) =13.94, $p<0.05$), where most women either had no idea or said the forest was very healthy (Figure 4.7a). Most respondents owning permanent houses thought the forest was in good condition while those with temporary houses mostly said that it was degraded citing depletion of building poles (Figure 4.7b). This argument also emerged in all the focus group discussions as well as from four out of six of the key informant interviews The focus group discussions also revealed an idea among the local communities that the *Rhizophora mucronata* (known locally as *mkoko*) in Mtwapa Creek are different from those found in other areas of the Kenyan coast due to what they term as extremely thick bark and crooked nature of the main stem. It was also established from the interviews that *Xylocarpus granatum* (*mkomafi*) and *Avicennia marina* (*mchu*) are quite rare within this mangrove swamp leaving the entire forest to be occupied predominantly by *R. mucronata*.

[▲] score is a bundle of firewood or building poles containing 20 pieces of wood. According to Mohamed (2008), one score of firewood is equivalent to approximately 0.15 ± 0.07 m^3.

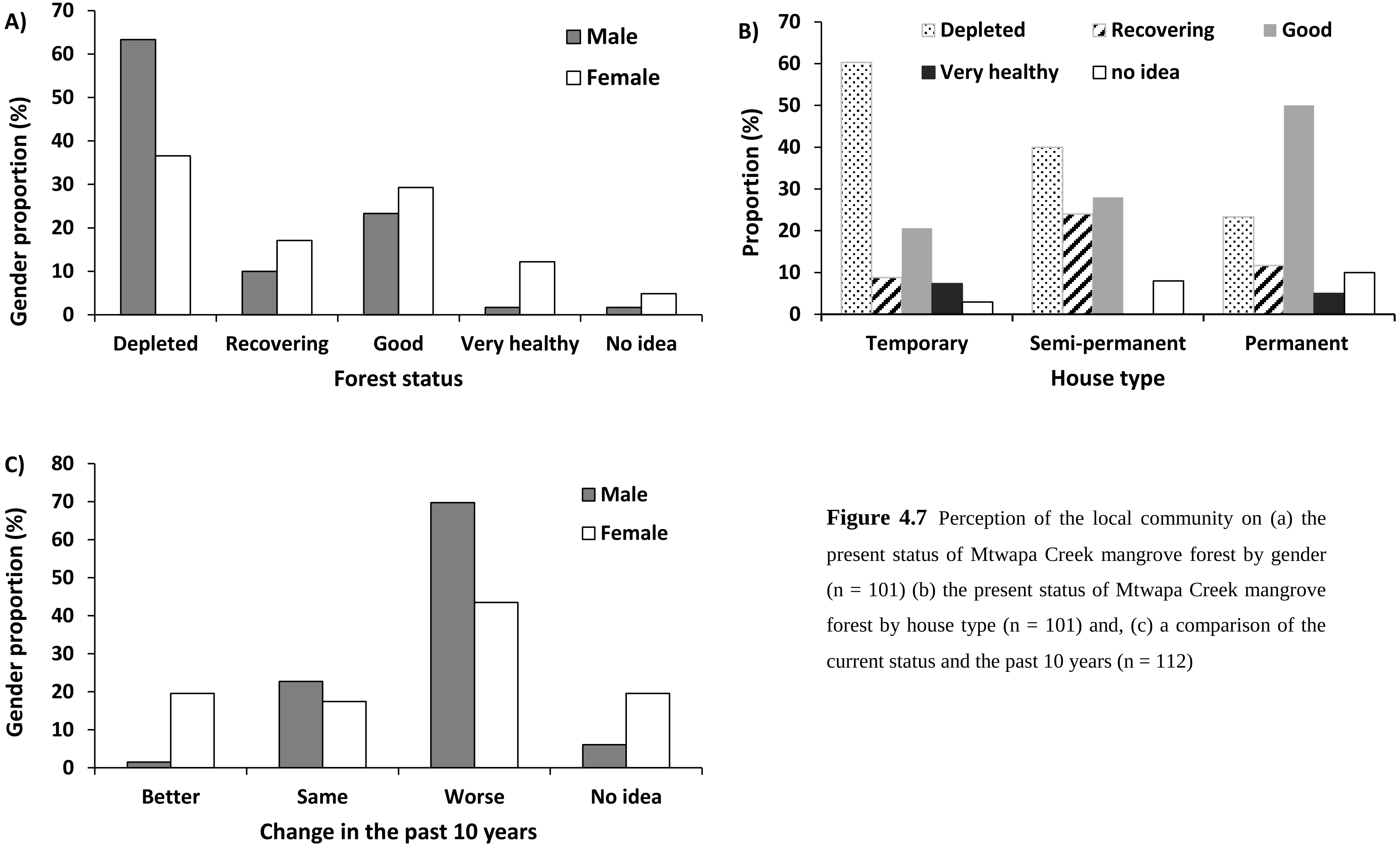


Figure 4.7 Perception of the local community on (a) the present status of Mtwapa Creek mangrove forest by gender (n = 101) (b) the present status of Mtwapa Creek mangrove forest by house type (n = 101) and, (c) a comparison of the current status and the past 10 years (n = 112)

When asked about their perception on change over the past 10 years, a large percentage of respondents (58.3% of those who were more than 24 years old at the time of interview) consider the forest status as getting worse. Only 8.3% consider it as better, while another 21.3% say there has been no change. Although there was no significant association between gender and the response given with regard to changes over the past 10 years, most women either had no idea or considered the forest better while men said there was no change or that the forest status had gotten worse (Figure 4.7c). The study also established that most men based their response on shortage of poles suitable for construction while women mainly considered cover change.

4.3.6 Perceived causes and effects of mangrove degradation

Various causes of degradation of mangroves in Mtwapa Creek were identified with cutting pressure being mentioned by 78.9% of the respondents. Out of this, 76.8% believed mangroves were getting destroyed entirely because of cutting while the rest said it was a combination of exploitation and other causes. Natural tree deaths and lack of rain or excess of it were the other factors mentioned by 10% of the respondents in each case. While only 1.4% of all the respondents mentioned sedimentation as a possible cause of mangrove degradation, of those who considered the mangrove forest as degraded (53%), forty three (43%) agreed to possible impacts of farming and sedimentation influence. In addition, the contribution of land based activities including farming and sewage and litter disposal were mentioned as adverse actions in both Mtomondoni and Mdengerekeni during focus group discussions.

The terrain around the mangrove forest is generally characterised by steep slopes yet as the survey established, the local communities farm closer to the creek where they say the soil is more fertile (Plate 3.1). An analysis of the proximity of the farms showed that of the interviewed farmers, 50-70 % of their farms were within 10-100 m distance from the highest spring water mark. Our observations revealed that other local communities were even ploughing on steep slopes facing the creek exposing the soil to erosion. It was also established that poor farming techniques contributed largely to the low fertility through erosion of top soils and frequent tilling of the same piece of land.

Plate 3.1 Some of the farming areas seen along Mtwapa Creek on the steep slopes facing the mangrove forest below. (*Picture by Nico Koedam, February 2011*)

Farming of maize, cowpeas and green grams was done in two cropping seasons a year, but this would vary interannually considerably due to unfavourable weather patterns. Other crops in the farms included: cassava, tomatoes, banana, pawpaws, mangoes and cashew nuts, all of which were grown in smallholdings for both subsistence and commercial purposes depending on scale. Other types of farming practised by the respondents were rearing of livestock and poultry keeping all which were mainly subsistence in nature.

While some respondents said the changes that have occurred in the mangroves of Mtwapa Creek have not affected their lives in any way, others believed the degraded nature of the forest has lowered their standards of living further. For instance respondents from Mtepeni argued that with more stringent measures put in place following the presidential ban in 2000, the charcoal burners in the village were forced to abandon the activity. The result has been a loss of income and consequently significant drop out of children from school due to the measures, a concern that was also expressed during the focus group discussions.

4.4 Discussion

4.4.1 Socio-economic status of local communities influence perception and dependence on mangroves

Most of the respondents from the five villages surveyed were middle aged men (Table 4.1). The variation in gender of the respondents is largely attributed to the cultural order in existence that conferred household headship (our target respondents) on the husband and not the wife. However, in certain instances the wife assumed headship in her partner's absentia occasioned by demise, divorce or occupational engagements. As a result, possible gender bias effects on successive results cannot be gainsaid. The fact that all respondents except two belonged to the native tribal group of the area may also have a bearing on the results. This is because natives are considered to be more informed on mangrove resources because of their wide range of local traditional knowledge and experiences that are linked with their historical dependency and continuity in coastal and marine resource use and associated customary management practices (Drew, 2005). Since the proportion of immigrants was too low, we cannot prove a distinction, but the findings at least align with it.

The low levels of education recorded in this study where most individuals possess only primary level education have also been reported by Samoilys *et al*. (2015) for the Kenyan coastal region in general. According to UNICEF reports, literacy levels among youths between 15-24 years old in Kenya was reported to be 81% between the years 2009 to 2013 (UNICEF, 2015). Primary school enrolment increased up from 63% to 84% upon the introduction of free education system between 1999 and 2011. Secondary education is however still wanting as out of the 60% enrolment, only 41% attend and that the transition rate from primary school in 2006 was only 50% (Ngware *et al.*, 2006; Global Education Fund news).

The mean household size values obtained in this survey are comparable to the county projections of 6.17 as per the 1999 population census which is regarded as large (Kilifi District Planning Team, 2000). Considering the household size hence large number of dependants (Table 4.1), it was clear that there is greater financial burden being imposed on those who are working to support the other members (Cinner and Pollnac, 2004). Further, the income levels reported in the area are far less than those reported 10 years earlier for the villages bordering Mida Creek in a similar ecological setting further north along the Kenyan coast (Zorini *et al.*, 2004). This suggests a significant reliance of the local human community on natural resources. Similar findings have been reported in other parts of the world where local communities particularly from developing countries tend to depend heavily on natural resources for livelihood due to their high poverty status (Cinner and Pollnac, 2004). Along the Kenyan coast, heavy dependence on marine resources had been reported by Cinner *et al*. (2010). Of the 18 indicators of wealth used, house type showed the most obvious association with the responses obtained from the respondents with most houses being of temporary structures and their occupants making most use mangrove goods.

Although there were multiple sources of livelihood identified in the Mtwapa Creek, farming was marked as the major source of income, a case also seen among local communities around Mida Creek (Gang and Agatsiva, 1992). Like in other parts of the Kenyan coast, many households had diversified their sources of income (Cinner *et al*., 2010), for instance, farming households were also engaged in small-scale businesses. Such diversification of livelihoods is viewed as a way of increasing income to households (Cinner *et al*., 2010). This is particularly important considering that Kenyan coastal areas have a greater percentage (62%) of its population living below poverty line[▲] ,with less than USD 1.25 (EUR 1.13) per day, (UNICEF, 2014) a situation replicated in Mtwapa creek villages. It would thus be an important area of focus considering that the 1st and the 15th Sustainable Development Goals (SDGs) lays emphasis on poverty alleviation and environmental conservation. As per the current international poverty line of USD 1.90 per day (Rist *et al*., 2016), the proportion of population living below the poverty line would be even bigger.

Utilisation of mangrove goods and services in Mtwapa Creek

The levels of knowledge of the local community about mangroves reported in this study is in agreement with findings by Naylor and Drew (1998), who noted that local communities living adjacent to a mangrove ecosystem have adequate working knowledge of mangroves attributed to their frequent interaction with the vegetation almost on a daily basis for their subsistence needs. In Kenya, mangrove trees have numerous traditional uses for both subsistence and commercial users, which varies with species type (Dahdouh-Guebas *et al*., 2000). The major uses highlighted in Mtwapa Creek (construction and fuelwood) show similarity in value attached to mangrove goods and services with other communities along the Kenyan coast (e.g. in South Coast of Kenya, Rönnbäck *et al*., 2007; in Mida Creek, Dahdouh-Guebas *et al*., 2000).

[▲] Poverty line established at less than 1.25 USD (EUR 1.13) per day as at the time the study was conducted.

Lack of woodlots in the area together with secondary data obtained from Kenya Forest Services (KFS) showing a progressive rise in illegal harvesting of mangrove wood for fuel over years (Figure 4.6d) may be an indicator of dependence on the adjacent mangrove forest for provision of cooking fuel. Generally in Kenya, fuelwood (charcoal and firewood) provides the main source of energy contributing 70% of energy demand in the National grid and 90% of the rural households use fuelwood (Githiomi and Oduor, 2012).

Local communities may however, rank these uses differently depending on site. Consequently, identification of mangrove goods and services, knowledge about mangroves and attitudes towards their conservation can vary significantly amongst user groups based on their gender, occupation and location (Rönnbäck *et al.*, 2007). Other than the role of mangrove in fisheries which was mentioned by a few respondents, under category ‘others’ (Figure 4.5), none of the ecological roles considered as very important globally in an expert survey (Mukherjee *et al.*, 2014) were mentioned suggesting a greater focus on the extractible benefits by the human community at local level. This also undermines the economic reasons for conserving nature as expressed by Balmford *et al*. (2002). Ecotourism was only mentioned by respondents who belonged to the conservation groups found within the Creek and are described in Okello *et al*. (2012).

Attempts by local respondents living around Mtwapa Creek to counteract illegal harvesting have been quite remarkable through the formation of environmental conservation groups (Okello *et al.*, 2012). Some of the interviewees were members of these groups who cited lack of support from the Kenya Forest Services and uncooperative non-members who thwart their conservation efforts. While they live close to the mangrove area and carry out alternative livelihood activities within the forest, they stand a better chance of arresting illegal harvesters; they do not have the power to do so. Under the new Forest Act, the local communities are now placed at the helm of managing forests through formation of Community Forest Associations (CFAs). This is however still at an infancy stage having only been formed in a few areas along the coast (Republic of Kenya, Draft 2015). A recent study by Frank (2014) showed major success in involvement of local communities in conservation of mangroves in Mida Creek further north of Mtwapa Creek.

Perception of local communities on forest status

A number of factors have been mentioned to influence how people perceive resources including migration, education and wealth (Cinner and Pollnac, 2004). In this study, gender, and wealth status greatly influenced the locals' opinion on forest status. The respondents viewed degradation based on two criteria: cover loss and pole size and quality. The largest proportion of respondents stated that changes in the mangroves are due to a decline in the desired sizes or overall tree density, similar to reports by Dahdouh-Guebas *et al*. (2000). Further, the fact that most of the respondents owning temporary houses claimed that the forest was depleted of poles suitable for construction could be attributed to their heavy dependence on the forest for building poles compared to those who had permanent houses. It has also been found that local communities rate natural mangroves highly than plantations due to the multiple goods and services they provide except for mangrove poles which are considered less durable in natural forests (Rönnbäck *et al*., 2007).

Despite lack of scientific backing, local communities' observation regarding poor form of *Rhizophora mucronata* (mkoko) in Mtwapa Creek corroborates the findings from the structural survey[▲] in chapter 2 of this thesis where it was noted that the forest was composed almost entirely of form 3 poles (poles unsuitable for construction). Additionally, their argument regarding scarcity of *Xylocarpus granatum* (mkomafi) within this mangrove swamp including *Avicennia marina* (mchu) which is otherwise common in other areas along the Kenyan coast is also in tandem with chapter 2. The rarity of the *A. marina* was attributed to death of the species at an early stage leaving the entire forest to be occupied predominantly by *Rhizophora mucronata*.

Perceived causes and effects of mangrove degradation

The study identified various causes of mangrove degradation with cutting pressure being singled out as the most important. Unsustainable exploitation and illegal extraction of mangrove trees particularly for timber, building poles and firewood has been cited as the major cause of historical decline in mangrove forests along the Kenyan coast (Dahdouh-Guebas *et al*., 2000; Kairo *et al*., 2001; Rönnbäck *et al*., 2007; Mohamed *et al*., 2008). This has seen a decline in mangrove forest cover, with the highest rate of loss being observed in the peri-urban areas (Mohamed *et al*., 2009; Bosire *et al*., 2013). However, together with the findings from chapter 3 of this thesis (increase in cover but poor pole quality); cryptic

---

[▲] Structural survey is the assessment of forest conditions focusing on regeneration and mature tree growth parameters in a given area degradation as also suggested by the local communities appears to be the major form of degradation in Mtwapa Creek. The fact that only *pau* and *vigingi* (Figure 4.6a and b) were allowed to be harvested before the ban may have equally compromised the structural stability of the forest with time (Kairo, 2001).

Apart from exploitation-related causes which are widely mentioned in literature, the respondents attributed mangrove degradation to natural tree deaths among other indirect causes. Such combination of threats could lead to degradation of mangrove ecosystems and consequently loss of the ecosystem services they provide (Dahdouh-Guebas *et al*., 2005a; Bosire *et al*., 2013). The local communities believe that the forest status may get worse or better depending on the line of action taken in terms of provision of alternatives, conservation including favourable policies and perfecting on participatory forest management.

4.5 Conclusion

This study contributes to understanding of the perception of local coastal communities with regard to the status of peri-urban mangrove systems and their future. The results bring out mixed opinions amongst local coastal communities on the past, current and expected future status of the mangrove forest. The results show that the difference in perception is associated with their gender, living standards, education level and knowledge about mangrove as a resource. Most concern is expressed by men who are less educated and live in temporary houses. This implies that in the implementation of management plans, perspectives of all stakeholders regardless of their status in the society should be integrated and a co-management approach be taken up. While the local communities engaged in various income generating activities they mainly depend on farming; which may indirectly affect the adjacent mangrove forest through possible sedimentation as suggested by the proximity to the creek and position of the farms with respect to the mangroves. Most of these activities, according to respondents, are aggravated by the high poverty rates in these villages, and any attempt to reverse these trends must entail economic empowerment in addition to natural science solutions - through technology and alternative livelihood sources. Nevertheless, awareness creation by various organisations and enforcement of law (though not fully effective) has played a considerable role in ameliorating degradation of the mangroves of Mtwapa Creek. Besides these, upscaling of existing conservation groups to ensure an effective a co-management approach to these resources is also recommended as has been seen in Mida Creek further north along the Kenyan coast.

PART III

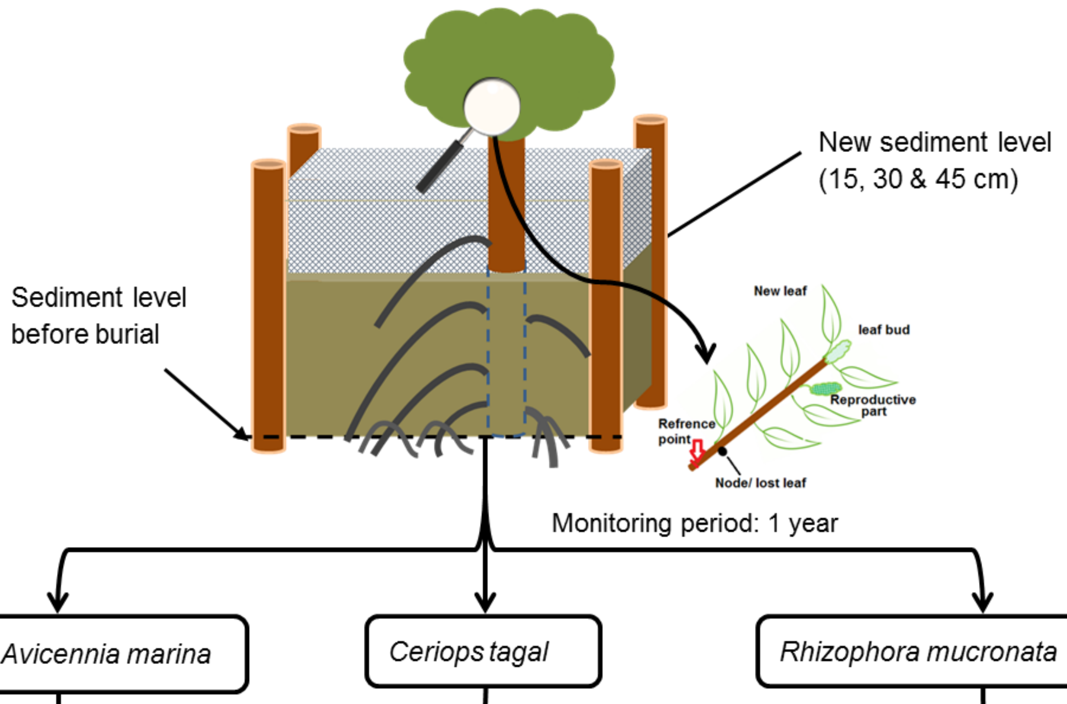
Experimental sedimentation in mangroves of Gazi Bay, Kenya

CHAPTER 5:

Effects of experimental sedimentation on the phenological dynamics and leaf traits of replanted mangroves at Gazi Bay, Kenya.

*Adapted from **Okello J.A.**, Robert E.M.R., Beeckman H., Kairo J.G., Dahdouh-Guebas F., Koedam N., 2014. Effects of experimental sedimentation on the phenological dynamics and leaf traits of replanted mangroves at Gazi Bay, Kenya. Ecology and Evolution 4(16):3187-3200.*

Graphical abstract



Avicennia marina

- Higher leaf emergence rates during wet season & lower during dry season in the partially buried trees compared to controls.

Ceriops tagal

- Increased leaf loss with burial during the first 6 months.
- Similar or higher leaf emergence rates than controls after the 2nd quarter.

Rhizophora mucronata

- Similar leaf emergence & loss as controls.
- Higher fecundity & productivity at sedimentation level 15 cm.

Under incidences of large sedimentation events, mangrove trees may capitalise on nutrient input associated with terrestrial sediment brought into the biotope thus maintaining the pattern of phenological events.

Contributors: Okello J.A.- main author; Robert, E.M.R., - write-up; Beeckman, H.- co-promoter; Kairo J.- experimental design & supervision; Dahdouh-Guebas, F.- supervision; Koedam N.- lead promoter, experimental design and supervision

Abstract

Background and aims: Sedimentation results in the creation of new mudflats for mangroves to colonise among other benefits. However, large sediment input in mangrove areas may be detrimental to these forests. The dynamics of phenological events of three mangrove tree species (*Avicennia marina*, *Ceriops tagal*, and *Rhizophora mucronata*) were evaluated under experimental sediment burial simulating sedimentation levels of 15, 30, and 45 cm.

Results: While there was generally no shift in timing of phenological events with sedimentation, the three mangrove tree species each responded differently to the treatments. Partially buried *A. marina* trees produced more leaves than the controls during the wet season and less during the dry season. *Ceriops tagal* on the other hand had higher leaf loss and low replacement rates in the partially buried trees during the first 6 months of the experiment but acclimatised with time, resulting in either equal or higher leaf emergence rates than the controls. *Rhizophora mucronata* maintained leaf emergence and loss patterns as the unaffected controls but had a higher fecundity and productivity in the 15 cm sedimentation level.

Conclusion: The results show that experimental sediment burial of adult mangroves elicited acclimative responses in crown foliage dynamics among buried trees. This emphasises resilience of the three studied mangrove tree species, reflected in the ability of maintaining the pattern of phenological events under incidences of large sedimentation events.

5.1 Introduction

The pattern of phenological events (flowering, fruiting, leaf emergence, and fall) is important in determining survival and reproductive success of plants. Moreover, leaf phenology constitutes an important aspect of studies concerning production and fluxes of organic matter in an ecosystem (Wium-Andersen and Christensen, 1978; Zalamea and Gonzalez, 2008). In addition, the shedding process provides a measure of organic input (Saenger and Moverly, 1985; Kristensen *et al.*, 2008; Zalamea and Gonzalez, 2008). As an indicator of plant responses to environmental conditions, phenology provides insights into how plant growth can be affected by these conditions (Sekhwela and Yates, 2007). Notably, changes in climatic conditions have resulted in a phenological shift in many species across various taxonomic groups due to global warming (e.g., Fitter and Fitter, 2002; Visser and Both, 2005; Trnka *et al.*, 2011). Consequently, certain plant species may experience earlier or delayed bud break, flowering, and/or fruiting, hence facing an increased risk for attack by seasonal pests or unfavourable weather conditions (Rochette *et al.*, 2004; Thampanya, 2006; Henniges *et al.*, 2007). Additionally, premature leaf fall (abscission) may also result from release of drought stress as has been witnessed in watered seedlings following severely dry conditions (Tudela and Primo-Millo, 1992; Gómez-Cadenas *et al.*, 1996).

Mangrove ecosystems form an ecotone between land and sea. As such, they are recipients of disturbances originating from both land and sea, including those due to climate change (Cahoon and Hensel, 2002; Dayton *et al.*, 2005). These disturbances (both natural and human induced) shape the ecosystem but also alter frequency and/ or duration of certain processes within the ecosystem (Dale *et al.*, 2001). An example is accretion, a natural process through which mangrove forests trap sediment facilitated by the complex aerial root network of the trees (Kathiresan, 2003; Alongi, 2009). Thus, mangrove forests may function as land builders by accumulating between one and eight millimeters of sediment annually (Kathiresan, 2003; Smoak *et al.*, 2013). In plantations of high density, the forests accrete up to 13 mm per year leading to an elevation increase of 2.8 mm (Kumara *et al.*, 2010; Kimeli, 2013). The deposition pattern may also vary spatially with distance from the seaward fringe (Kimeli 2013). As mangroves accumulate sediment, the long-term effect is rise in elevation which would also be important in increasing the capacity of these forests to keep pace with sea level rise (Kumara *et al.*, 2010; Friess *et al.*, 2012; Smoak *et al.*, 2013).

Sediment accretion is, however, greatly influenced by disturbances including anthropogenic activities and natural disasters. For example, due to additional warming of the globe, extreme downpours have now become more frequently associated with climate change (Caldeira 2012). This may ultimately lead to an even higher sediment load in the mangrove areas as flooding increase discharge of the same with even up to 10 cm level deposit during a single downpour event (Bamroongrugsa and Yuanlaie 1995). In Kenya, up to 1.4 m depth of terrigenous sediment was deposited in Mwache Creek after the 1997 – 1998 El Niño rains (Kitheka *et al*., 2003) that left behind 200 ha of mangroves dead (Bosire, 2006). Run off from land has additionally been aggravated by exposure of land to erosion through widespread deforestation in the catchment areas (Panayotou, 1993; Pfeifer *et al.*, 2012) as well as other human activities such as poor farming practises along the riparian zones (Harty, 2009). It is therefore prudent to understand the impact of such events on important mangrove tree species' growth and development processes such as phenology.

A number of studies on forest disturbance have focused on the ability of mangrove species to disperse (Rabinowitz, 1978; Clarke, 1993; De Ryck *et al.*, 2012) and to tolerate temperature and moisture changes (Yáñez-Espinosa and Flores, 2011). Sedimentation effects on young mangrove trees (seedlings/ saplings) have also been evaluated in a number of studies (Terrados *et al.*, 1997; Thampanya *et al.*, 2002; Friess *et al.*, 2012). The only attempt to document impacts of partial burial by sediments (dieback and death) on mature trees is by Ellison (1998). This is however an anecdotical report from a number of locations (Table 5.1) leaving uncertainties on whether there exists a threshold below which normal tree functioning is assumed before they succumb to the increase in sediment level. This chapter and the two subsequent ones attempt to address this gap by looking at physiological and morpho-anatomical response of three mangrove tree species to selected increased level of sedimentation.

Table 5.1 Summary of sediment burial in mangrove trees (*Avicennia marina* and *Rhizophora* sp.) and consequences. Reproduced from Ellison (1998).

Species	**Location**	**Burial depth**	**Effect**
*Avicennia**	Singapore	10 cm	Death
	Princess Charlotte Bay	70 cm	Survived
Avicennia marina	Gladstone	5 cm	Stressed
	Bowen	12 cm	0.5 ha death
	Port Samson	20 cm	Death
	Gladstone	50 cm	Death
	Sinai	50 - 200 cm	Unhealthy
	Saudi Arabia	?	Unhealthy
	Australia Mud Island	?	Death
*Rhizophora**	Princess Charlotte Bay	70 cm	Survived

(*) The specific name of the mangrove is not given; (?) information is lacking

In this section, crown foliage dynamics of three common and wide ranging mangrove species, that is, *Avicennia marina* (Forssk.) Vierh., *Ceriops tagal* (Perr.) C.B. Rob. and *Rhizophora mucronata* Lam., subjected to experimental sedimentation is examined over a period of one year. The study aims at improving the understanding of mangrove forests' resilience to extreme environmental conditions and the influence of large instantaneous sedimentation events on productivity and organic matter dynamics in this ecosystem. Herewith, important information for up-scaling silvicultural practises in mangrove forests, thus ensuring sustainable management of this resource, is provided. The study hypothesised that increase in sedimentation will only result in death of mangroves when a threshold is surpassed and that below this level the cycle of phenological events and productivity will not be affected.

5.2 Materials and methods

5.2.1 *Study site and species*

The experiment was set up in plantations of *C. tagal*, *R. mucronata* and *A. marina*. The trees were planted in 1994, 1998 and 2001 respectively at Gazi Bay (4º22′S, 39º30′E), 55 km south of Mombasa in Kenya (Figure 5.1). Whereas the *C. tagal* and *A. marina* plantations were established following over-exploitation that left the area bare, *R. mucronata* was replanted after the 1997 - 1998 El Niño rains.

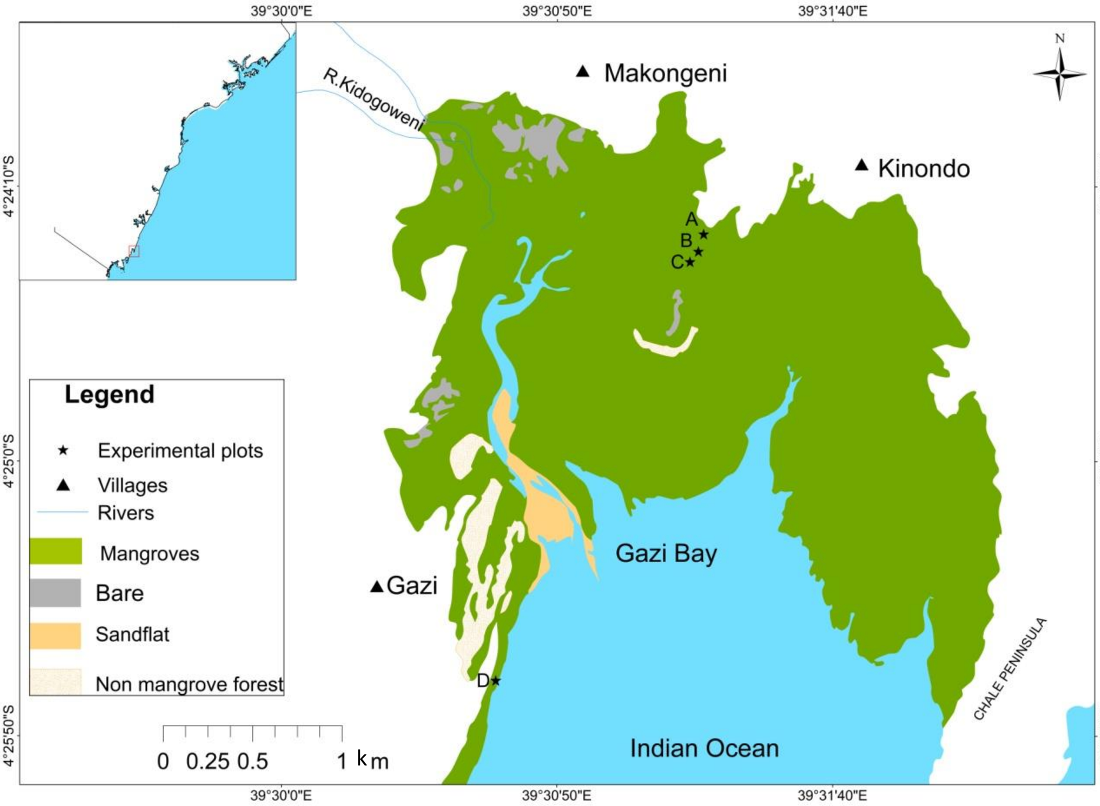


Figure 5.1 Map of Gazi Bay locating the different study sites: A - *Avicennia*, B - *Ceriops* landward, C - *Ceriops* seaward and D - *Rhizophora*. The inset shows where the study area is located within Kenya (Kenya Marine and Fisheries Research Institute database).

All the three species were replanted in sites where they occurred before following the appropriate respective inundation classes and adjacent to natural stands of the respective species. The species selected for this study make up the dominant formation of mangroves in Gazi Bay (Matthijs *et al.* 1999; Neukermans *et al.* 2008). The mangrove forest is approximately 615 ha (UNEP, 2001; Neukermans *et al.* 2008) covering about 34.2% of the 1800 ha bay (Slim *et al.* 1996). The bay has a semi-diurnal tidal regime with amplitude of ca. 4.0 m at spring tide and 0.7 m at neap tide (Hemminga, 1994).

The climate of the area is characterized by a bimodal distribution of precipitation (Lieth *et al.*, 1999). A distinct dry season (December – March) is followed by a long (April – July) and a short rainy season (October – November). The study was conducted between January 2011 and November 2012 (Appendix Table S2) in which a similar scenario was observed (Figure 5.2). However, the dry season in 2011 was relatively wet and there was an unusually high amount of rainfall during the transition between long rains and short rains as compared to that averaged in Lieth *et al*. (1999). During the study period, the heaviest downpour was experienced in the short rainy season (October 2011 and November 2012; Figure 2).

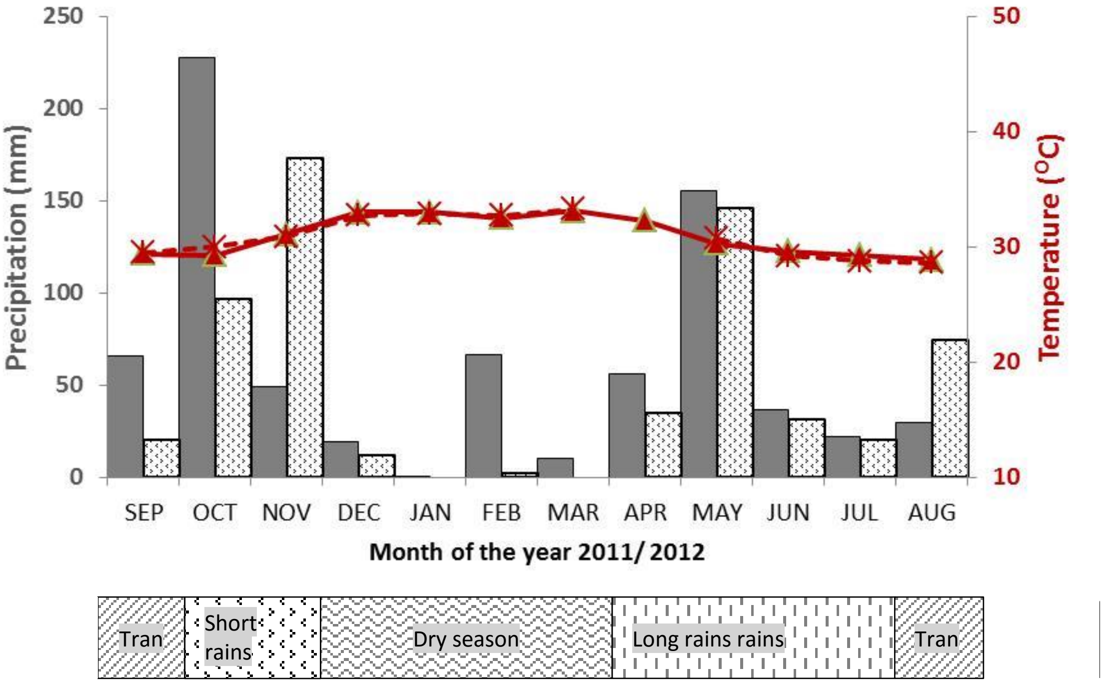


Figure 5.2 Monthly precipitation (mm - left Y axis) and mean monthly maximum temperatures (°C - right Y axis) at Mombasa from September to August 2011 [▬ /—▲—] and 2012 [▨ /- -✱- -] based on data from the Kenya meteorological department, Ministry of Environment and Mineral Resources, Nairobi, Kenya. The dry season (December – April) was relatively wet in 2011 and the transition (Tran) between long and short rains (August-September) were equally wet as compared to means obtained by (Lieth *et al.*, 1999) during the same months.

5.2.2 *Experimental design*

The study involved setting up experimental plots that mimic a scenario of instantaneous sedimentation in mangrove forests. Squared plots of 2 m by 2 m were selected within the plantations and randomly assigned to the treatments purposely avoiding trees on the outermost edge of the plantations. A set of four plots were selected per species except for *C. tagal* where the area of the plantation was large enough to accommodate two sets, four closer to the plantation edge and another four located about 20 m from the margin. For the purpose of this experiment the former is referred to as landward and the latter as seaward (Figure 5.1). Under natural setting, *C. tagal* also occupies such positions within the tidal flat in the study site.

The selected plots were surrounded with a netting material of 0.5 mm mesh size fixed at a depth of 10 cm and constrained to the ground using wooden pegs to avoid leakage of sediment out of the enclosure (Plate 5.1b). Enclosures were then filled with terrestrial sediment (mainly sandy loam) from adjacent upstream areas to levels of 15 cm, 30 cm and 45 cm excluding the control, where no sediment was added, but with the same net and pegs used (Plate 5.1b, 5.1c). These sediment levels (treatments) were selected based on studies of normal accretion rates listed in a review by Kathiresan (2003), adjusted to include the lowest ranges within which Ellison (1998) recorded mangrove dieback and mortality in *A. marina* in various areas (Table 5.1) and sedimentation levels recorded in Mwache Creek, Kenya during the 1997 – 98 El Niño rains. The height of each mesh was such that an allowance of approximately 10 – 15 cm was left at the top after adding respective quantity of sediment per treatment. During the first two weeks subsidence was experienced and refilling of sediment was done to ensure the treatments are maintained as originally designed throughout the experiment. Benthic fauna was allowed to colonize (decapods, mollusks) and more generally spoken all plots were left to undergo full influence of natural mangrove processes (litter accumulation, natural regeneration and tidal influence).

The plot sizes were designed in such a way as to include at least two central trees in the enclosure. Even when many trees were included in the enclosure, only trees that were expected to experience as little as possible edge effect were selected for monitoring (Appendix I Table S3). Each of the selected trees was considered as replicates of each other in terms of tree responses in all the plots. The selected trees were marked accordingly for subsequent monitoring. On each of these trees, six shoots were selected randomly aligned from the tree crown top to the bottom and marked at about 10 cm from the tip (reference point). The set ups were done at different times and as such the experiments did not run concurrently in the three study species (Appendix I Table S3). *C. tagal* was set in December 2010, *A. marina* in April 2011, while *R. mucronata* was done in October 2011 (Appendix I Table S3).

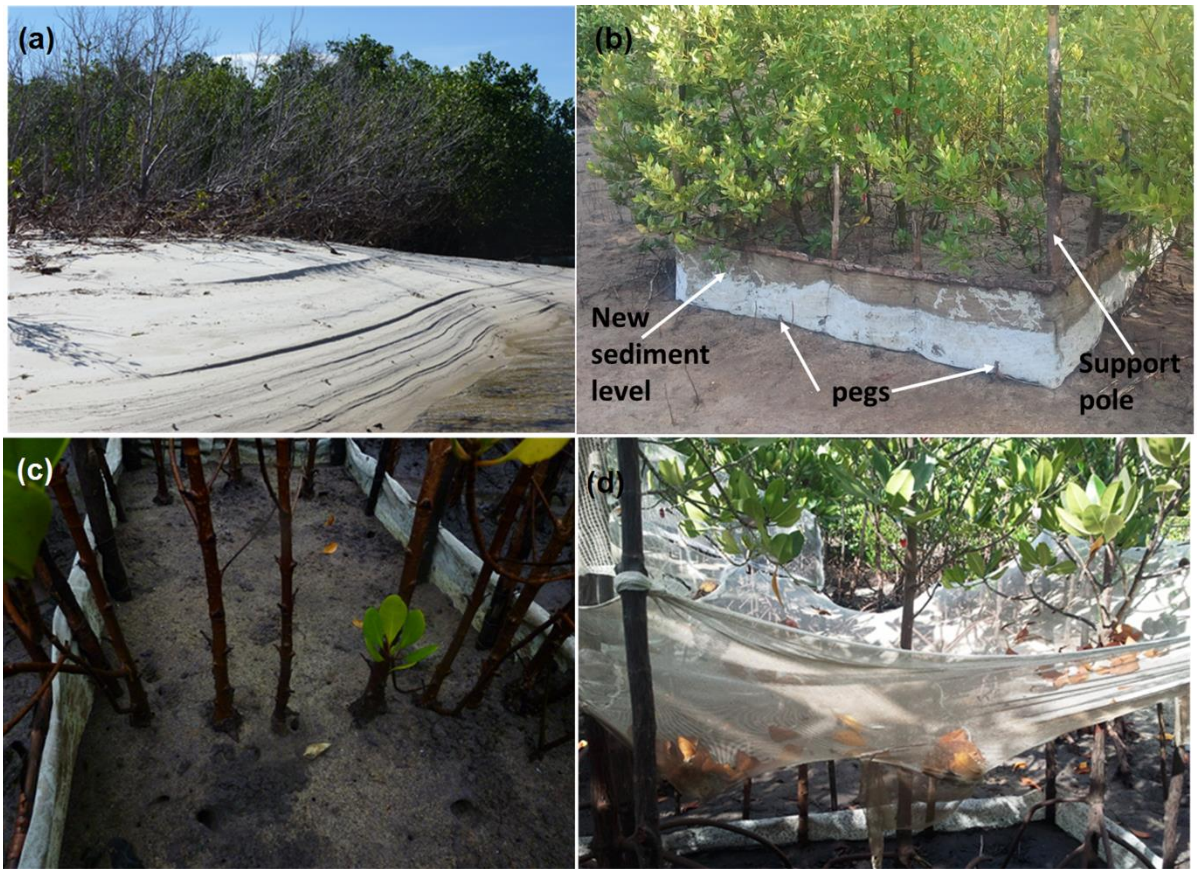


Plate 5.1 (a) A section of *Sonneratia alba* plantation in Gazi Bay dying from continuous natural sedimentation through wave and wind deposition; **(b)** *A. marina* trees partially buried with terrestrial sediment in one of the experimental plots; **(c)** Crab burrows in a 30 cm level of experimental sedimentation in *C. tagal*; and **(d)** *R. mucronata* enclosure with litter trap in one of the experimental plots. (*Pictures by Judith Okello, 2012*).

5.2.3 *Tree variables and phenological monitoring.*

At the start of the experiment, tree heights were measured using a calibrated pole. Diameter measurements were carried out at 30 cm above the highest prop root in *R. mucronata* (D_{130} *sensu* Brokaw and Thompson, 2000). In *C. tagal* and *A. marina*, the trees were barely 2 m in height and diameter measurements were done at 30 cm above ground (D_{30}) and at half tree height ($D_{1/2}$). Whenever branching (multiple stems) occurred below 30 cm tree height, each of the branches (stems) was treated as a separate individual tree (Appendix Table S3).

On the selected tree shoots, all leaves present at the start of the experiment were numbered consecutively on the adaxial surface using a permanent marker pen. The marks were made as small as possible to minimise any adverse effect on the leaf. Monthly, new leaves were assigned the next number and nodes as well as reproductive parts located. Assessment of crown growth was done by measuring apical increment of the same shoots as well as by monitoring development of new sub-shoots. Monitoring began one month after establishment of the experiment and lasted over a period of one year (Appendix Table S3).

Litter fall in *R. mucronata*

Litter production of *R. mucronata* was determined by collection in 2 m by 2 m traps made of hardware net material with a 2 mm mesh size tied to poles erected at each corner of the plots (Plate 5.1). These traps were suspended horizontally below the canopy of the shortest tree in the plot but high enough to avoid soaking during high tide (Plate 5.1d). Weights were placed in the traps at an angle to create a depression of about 30 cm ensuring that no litter collected spilt out. Litter was emptied from the traps biweekly during the first four months then monthly afterwards and sorted into leaves, reproductive parts (flower buds, flowers and fruits) and woody materials (shoots, twigs and bark pieces). The samples were weighed and then dried in the oven at 70 °C until a constant mass was obtained. After obtaining the required results, all the litter were emptied back to the respective plots.

Leaf traits

At the end of the field experiment, 20 mature leaves were selected randomly from each of the sample trees of all three species within the following conditions: i) leaves formed during the experimental period and ii) leaves more or less equally exposed to sunlight. The petioles were carefully cut off and each leaf scanned individually to determine the surface area using a Portable Laser Leaf Area Meter (CI-202, CID Bio-science, Washington, USA). The leaves were then pooled per tree, weighed and oven dried at 70 °C until a constant mass was obtained from which the degree of succulence was determined. This was calculated by subtracting leaf dry weight per unit area from wet weight per unit area (Longstreth and Nobel, 1979). The tendency to succulence provides a measure of water and nutrient preservation capacity by leaves particularly common among trees growing in water and nutrient limited sites.

5.2.4 *Environmental variables*

Sediment physicochemical parameters (porosity, interstitial water salinity and redox potential) were measured three months after establishment of the experimental set-up. Repeated salinity measurements were done monthly for another three months and redox potential redone after six months. Interstitial water was collected using a punctured plastic tube connected to a vacuum pump and salinity measurements were done with a hand-held refractometer (ATAGO, Tokyo, Japan). Redox measurements were done using a portable pH/ORP meter with ATC and hold feature (HI 8424, Hanna instruments, USA). Sampling was done at 15 cm depth (top 15 cm) and at 15 cm below the interphase of the added sediment and the original ground level. Soil porosity was determined as in equation 1, following PUMPSEA (2005).

$$\text{Porosity} = \frac{Soil\ water\ content * density}{100} \qquad \text{eqn 1}$$

Where,

$$\text{Water content} = \left(\frac{wet\ weight - dry\ weight}{Wet\ weight}\right) * 100 \qquad \text{eqn 2a}$$

and

$$\text{Density} = \frac{Mass\ of\ wet\ sediment}{Volume} \qquad \text{eqn 2b}$$

The height above datum of the plots was determined with the help of large tracing paper painted with water soluble ink that were tied on to tree stems adjacent to each plot before high tide. The positioning of the tracing papers on the trees was estimated based on the highest tide levels obtained from tide tables (Tide table: Kilindini harbour, Kenya). Water levels after high tide were measured from the demarcation left on the tracing paper by water washing away the ink and height above datum/mean sea level (AMSL) was calculated as:

$$\text{AMSL}= (MHWL - water\ level\ at\ site\ with\ respect\ to\ the\ ground\ ) + plot\ sedimentation\ level \qquad \text{eqn 3}$$

Where MHWL (mean high water level) is the high tide reading from the tide table (Kilindini harbour, Kenya).

Inundation frequencies were assigned according to Watson (1928) and given in Appendix S2. Redox potential values were within the ranges associated with higher inundation classes (Matthijs *et al.*, 1999). The redox potential ranged between -54 and 50 mV in *C. tagal* and *R. mucronata* plots and 34 to 318 mV in *A. marina* plots.

5.2.5 *Data analysis*

Mean monthly leaf flushing, mean monthly leaf loss, leaf replacement and shoot increment as well as percentage of shoots with reproductive parts were determined from the collected data. Leaf flushing and loss data were first tested for correlation with precipitation pattern and experimental period and categorised accordingly. *Avicennia marina* leafing pattern were therefore categorised based on precipitation pattern while in *C. tagal* grouping was based on experimental time frame. Where no notable relationship was obtained (as in *R. mucronata*) data grouping was done according to precipitation pattern. The length of time taken for a shoot to drop a leaf gained during the study period was designated leaf longevity. Fecundity was calculated as described by Hegazy (1998), where:

Flowering success = (number of flowers/total number of reproductive units) x 100;

Fruiting success = [number of fruits/ (∑(number of flowers + fruits)] x 100.

The reproductive units represent the sum of flower buds, flowers and fruits.

Results for landward and seaward *C. tagal* were pooled for subsequent analysis in all variables except leaf flushing for which there was significant difference between the two blocks.

Data sets were tested for normality and homogeneity of variance and since these assumptions were not met even after log transformation, Kruskal-Wallis ANOVA by Ranks tests were used to determine significant differences among treatments. This was followed by a pairwise comparison of the four treatments using multiple comparison of mean ranks whenever significant difference was noted at $p = 0.05$. In addition, a Mann-Whitney U test was used to test for differences in leafing between the wet months and dry months and Spearman rank order correlations were done to determine relationship between variables and level of sedimentation where there was significant difference across treatments. All statistical analyses were done in STATISTICA 7.0 (StatSoft Inc., Tulsa, USA).

5.3 Results

5.3.1 *Leaf flushing and leaf loss*

A Kruskal-Wallis analysis revealed significant influence of season ($H= 17.86$, $p < 0.01$) as well as sedimentation levels ($H= 22.98$, $p < 0.05$) on leaf emergence in *A. marina*. Whereas the controls maintained similar leaf emergence rates over the different seasons ($U= 135.5$, $p > 0.05$ Mann-Whitney U test), there were significantly higher rates of leaf emergence in the partially buried *A. marina* trees during the periods with the highest precipitation rates as opposed to the dry months (Figure 5.3a; $U= 302$, $p < 0.05$, Mann-Whitney). There was also a general reduction in leaf emergence rates during the dry season with the controls being less affected (reduction of 17.75%) as compared to the silted trees (15 cm:– 71.88%, 30 cm:–

47.23% and 45 cm:– 48.68%) resulting in thinner crowns. Leaf loss in this species was relatively higher during the dry season in controls and 15 and 45 cm sedimentation levels but the same increase experienced during the short rains in the 30 cm level (Figure 5.3b).

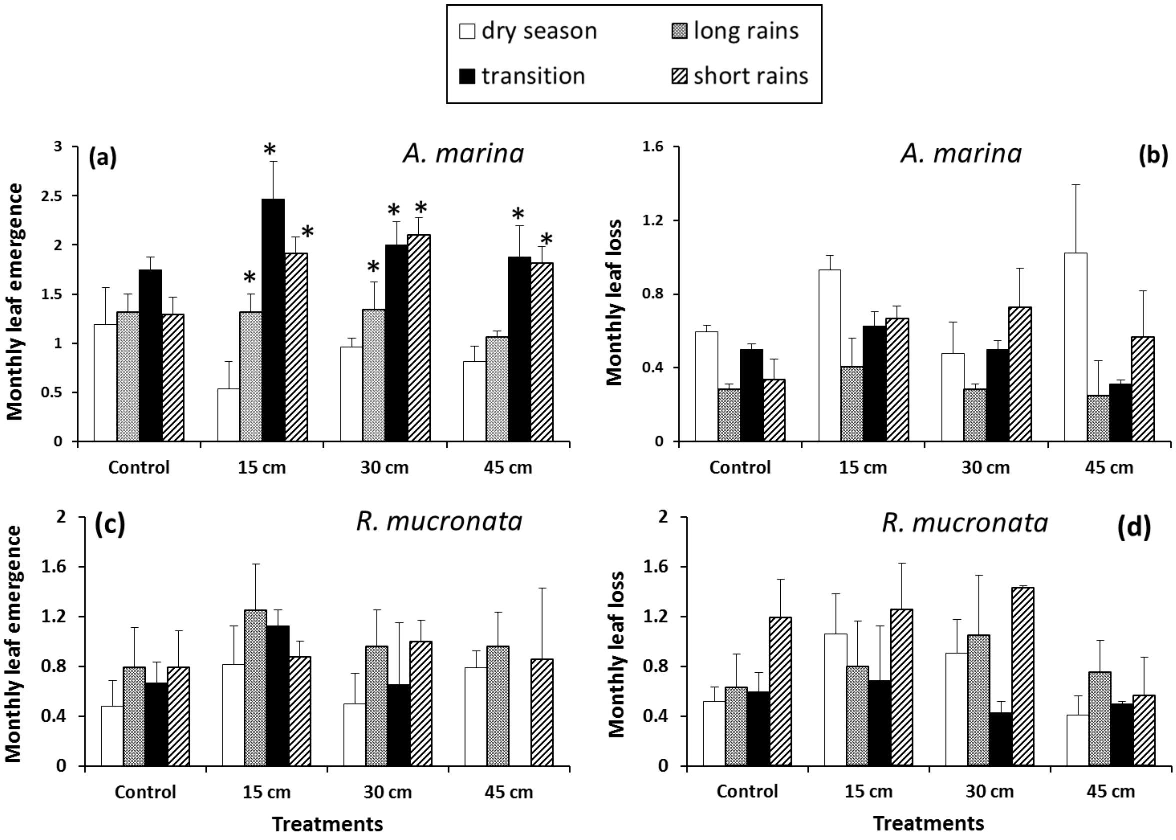


Figure 5.3 Mean (±SE) monthly leaf emergence **(a, c)** and leaf loss **(b, d)**, in *A. marina* and *R. mucronata* growing under different experimental sedimentation levels (15, 30, 45 cm) between June 2011 – May 2012 in *A. marina* and November 2011 – October 2012 in *R. mucronata*. The wet season was taken to include the period of long rains, transition and short rains. *Marked bars are significantly different from the dry season

Additionally, percentage number of shoots with leaf replacement rate higher than leaf loss rate was higher in the controls during the dry season and highest in the 15 cm partially buried trees during the wet months (Figure 5.5).

Ceriops tagal trees displayed a bimodal leaf emergence pattern with a significant drop in leaves gained during the third quarter of the experiment (August – September, 2011) in both landward and seaward plots (Figure 5.4a and b). In the landward *C. tagal*, leaf emergence was lower in the 45 cm silted trees than the rest of the treatments during the first 3 quarters of the experiment (February – September 2011) with a significant reduction in the second quarter (H= 15.12, $p < 0.01$). By the fourth quarter of the experiment, partially buried trees from all the levels in landward plots had relatively higher leaf emergence rates than the controls (Figure 5.4a). In the seaward plots, significantly lower leaf emergence rates were observed in the partially buried trees during the second quarter ($H= 9.77$, $p < 0.05$) with 45 cm sedimentation level showing significantly lower rates than the controls ($p < 0.05$, multiple comparison of mean ranks). Leaf loss in this species was significantly higher in the partially buried trees as compared to the controls ($p < 0.001$). This was however only during the early phase of the study period (1^{st} quarter; $H= 31.95$, $p < 0.001$; 2^{nd} quarter: $H= 38.79$, $p < 0.001$) after which all the treatments experienced similar leaf loss rates (Figure 5.4c).

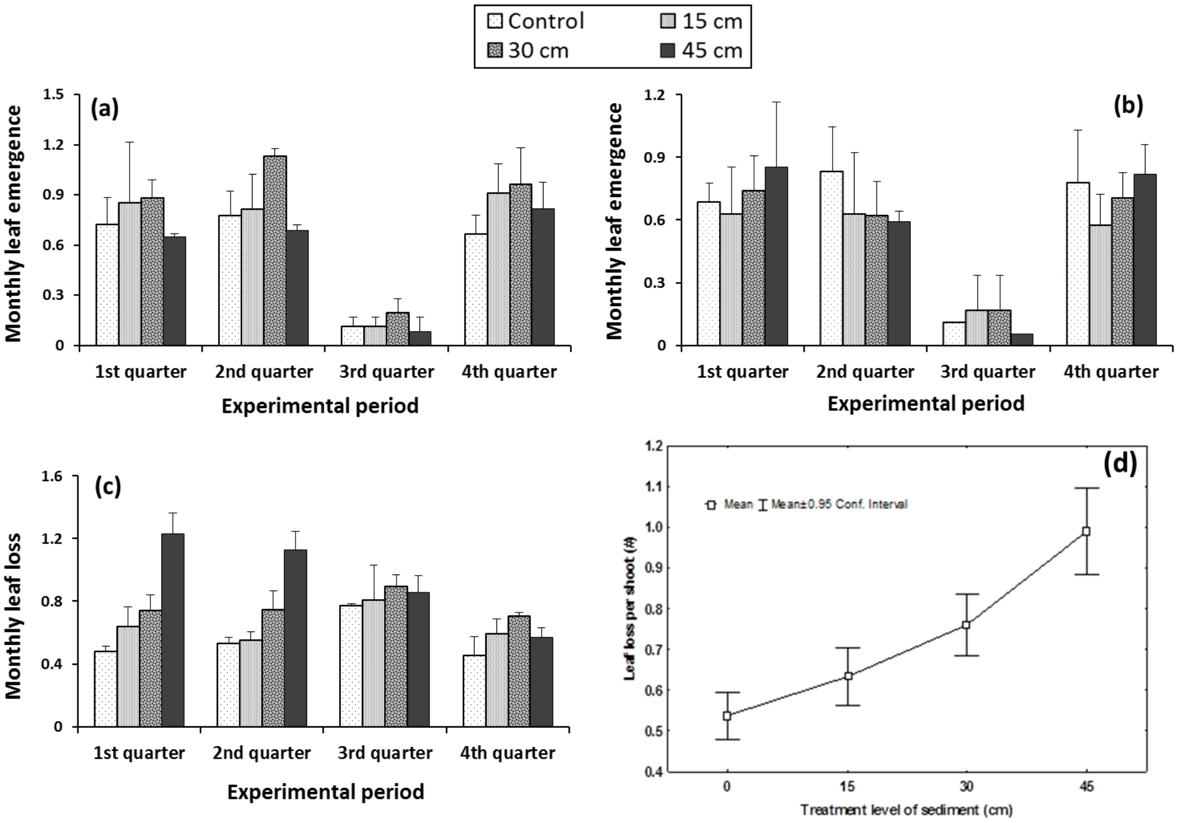


Figure 5.4 Mean (±SE) monthly leaf emergence **(a, b)** and mean (±SE) monthly leaf loss **(c)** in *C. tagal* mangrove trees growing under experimental sedimentation during the 1^{st} quarter (February – April), 2^{nd} quarter (May- July), 3^{rd} quarter (August – September) and 4^{th} quarter (October – December) of the experimental period in 2011. **(d)** Overall mean (point) monthly leaf loss and 95% confidence interval (whiskers) among the different sedimentation treatments over the entire study period.

The rate of acclimatization in *C. tagal* with time was also with respect to sedimentation levels where the least buried trees (15 cm) were first to achieve reduced leaf loss by the second quarter (Figure 5.4c). When seasonality was not considered, and although a Spearman rank order correlation between levels of sedimentation and mean leaf loss per shoot was not strong (r_s (2869) =0.1437, $p < 0.05$), the results showed a progressive increase in leaf loss with increased in sedimentation reaching exceptionally high values in the 45 cm partially buried trees (Figure 5.4d). In addition, leaf replacement rates in *C. tagal* was significantly lower in the 45 cm partially buried trees as compared to all the other treatments during both the first (H= 20.28, $p < 0.001$) and second quarter (H= 25.32, $p < 0.001$) (Figure 5.5).

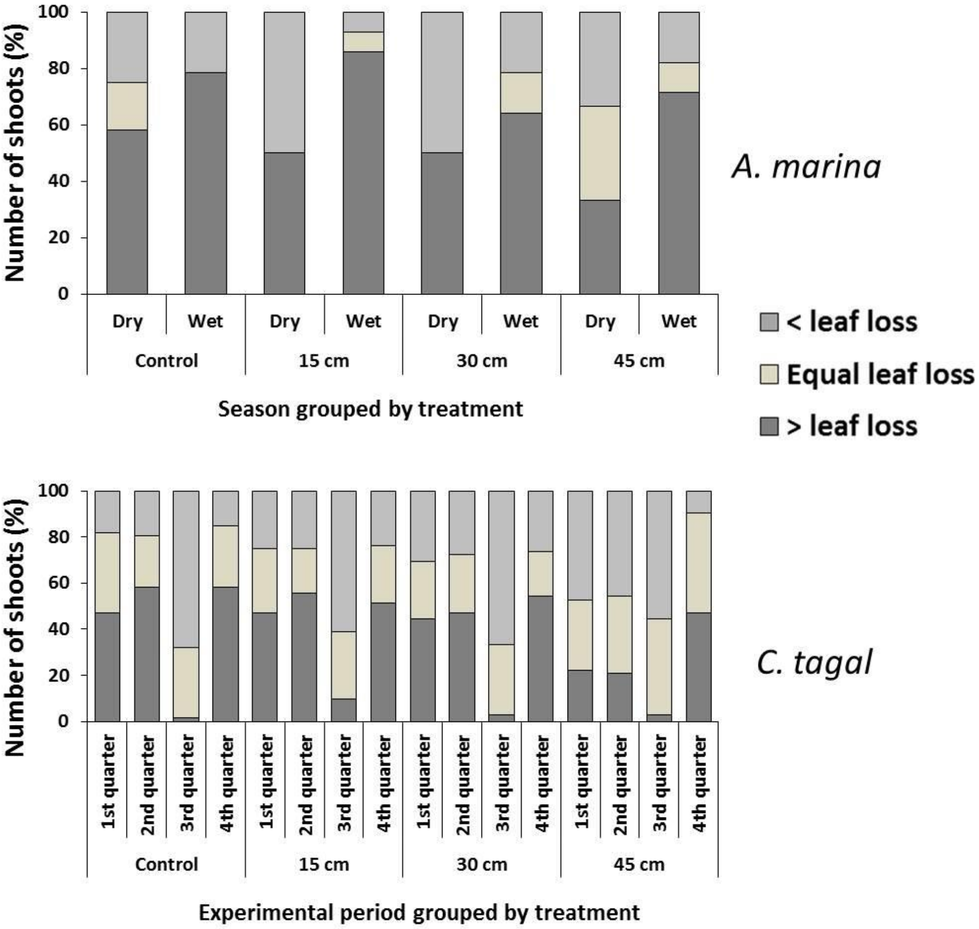


Figure 5.5 Rate of leaf replacement in *A. marina* and *C. tagal* expressed as a percentage number of shoots with leaf emergence rates less than, equal or greater than the rate of leaf loss in trees exposed to experimental sediment burial simulating three levels of sedimentation (15, 30, 45 cm).

In *R. mucronata*, there was no distinct peak in leaf emergence during the entire monitoring period (Figure 5.3c). In this species, there was a general alternation of peaks of decreased and increased leaf loss over the study period (H= 27.48, $p < 0.01$), with decreased leaf loss experienced in both the dry months, January – February, 2011 and wet season, July – September, 2011 (Figure 5.3d). However, the variations were more or less uniform among the treatments with no significant difference observed in either of the seasons ($p > 0.05$).

Leaf longevity was greater than 12 months in *A. marina* and *R. mucronata* but less than 12 months in the 45 cm silted *C. tagal* trees.

5.3.2 *Leaf size, succulence and shoot elongation*

Partially buried trees had leaves with larger surface area in all levels of sedimentation (*R. mucronata*) and up to 30 cm (*A. marina*, *C. tagal*) above which smaller leaves than those of controls were produced (Table 5.2). Leaf succulence remained similar in all the treatments as sedimentation did not show any notable influence on this parameter in the three studied species (Table 5.2).

Table 5.2 Mean (±SE) leaf surface area, leaf succulence, monthly shoot elongation and fecundity in the three studied mangrove tree species after one year of exposure to sediment burial simulating three levels of sedimentation (15, 30, 45 cm). Marked values are significantly different from controls at $p < 0.05$ (*) and $p < 0.01$ (**)

Species	Treatment	Leaf surface area (cm^2)	Leaf succulence (g dm^{-2})	Shoot elongation (cm month^{-1})	Fecundity	
					Flowering success (%)	Fruiting success (%)
A. marina	Control	7.46 ± 0.39	2.17 ± 0.15	1.27 ± 0.34	13.89 ± 2.78	4.04 ± 2.17
	15 cm	8.81 ± 0.41	2.07 ± 0.21	2.51 ± 0.63*	49.60 ± 12.61*	19.44 ± 10.02*
	30 cm	9.59 ± 0.51*	3.21 ± 0.84	2.35 ± 0.36	62.75 ± 12.59*	42.51 ± 21.30**
	45 cm	7.22 ± 0.31	2.26 ± 0.48	2.22 ± 0.59	66.03 ± 13.83*	27.56 ± 15.94*
C. tagal	Control	11.61 ± 0.42	3.37 ± 0.23	0.10 ± 0.03	48.56 ± 11.23	52.4 ± 23.76
	15 cm	13.74 ± 0.63	3.60 ± 0.19	0.08 ± 0.02	53.45 ± 21.54	47.78 ± 19.83
	30 cm	12.51 ± 0.43	4.14 ± 0.34	0.08 ± 0.02	46.47 ± 14.03	51.53 ± 20.37
	45 cm	9.77 ± 0.42*	4.08 ± 0.28	0.08 ± 0.01	54.68 ± 23.89	53.45 ± 21.87
R .mucronata	Control	34.21 ± 1.49	3.87 ± 0.18	0.16 ± 0.02	25.09 ± 12.96	21.56 ± 23.78
	15 cm	40.44 ± 1.71	3.87 ± 0.19	0.19 ± 0.02*	65.34 ± 19.04**	54.37 ± 10.93*
	30 cm	43.25 ± 1.95*	4.04 ± 0.29	0.17 ± 0.03	26.53 ± 15.74	24.52 ± 11.67
	45 cm	39.04 ± 1.65	3.37 ± 0.04	0.18 ± 0.03	28.64 ± 12.20	22.32 ± 10.45

Shoot elongation rate was significantly higher in the 15 cm partially buried *A. marina* trees as compared to the controls ($H= 14.62$, $p < 0.05$), with decreased growth observed in the 45 cm sedimentation level (Table 5.2). Similarly, *R. mucronata* there were significantly higher shoot growth in the lower sedimentation level ($p < 0.05$) but the values remained similar to those in the control with higher levels of burial (Table 5.2). There was no distinct peak in shoot elongation observed over the experimental period. In *C. tagal* the partially buried trees and controls had similar shoot elongation rates.

5.3.3 *Reproduction and litterfall*

Reproduction occurred at different times of the year among the species and there was no distinct shift in timing across the treatments in *C. tagal (*Table 5.3).

Table 5.3 Reproduction and leaf gain and leaf loss timing in the current study compared to a past phenology study conducted in Gazi Bay, Kenya. The earlier studies compared phenological trends of reforested mangroves against natural forests and *R. mucronata* reforested site is the same site where the current experiment was set up but had no sedimentation impact.

Species	Treatment	Peak reproduction		Leaf dynamics		Source
		Flowering	Fruiting	max leaf fall	max leaf gain	
A. marina	Natural	Feb-Mar & Dec	Apr-May	Aug-Oct	May-Aug	(Wang'ondu *et al.* 2010)
	Replanted	Jan-Apr & Dec	Mar-May & Jul-Sept	Feb & Aug-Nov	Feb & Aug-Nov	(Wang'ondu *et al.* 2010)
	Control	Feb-Apr	Apr-May	Dec-Jan	May & Aug-Oct	This study
	15 cm silted	Oct-Jan 2012	Feb-Mar	Dec-Jan	May & Aug-Oct	
	30 cm silted	Oct-Jan	Jan-Feb	Jun-Aug	May & Aug-Oct	
	45 cm silted	Oct-Jan	Feb-Mar	Dec-Feb	May & Aug-Oct	
C. tagal	Control	Multiple peaks	Feb-Apr	multiple peaks	Apr-Jun & Oct-Nov	This study
	15 cm silted	Multiple peaks	Feb-Apr	multiple peaks	Apr-Jun & Oct-Nov	
	30 cm silted	Multiple peaks	Feb-Apr	multiple peaks	Apr-Jun & Oct-Nov	
	45 cm silted	Multiple peaks	Feb-Apr	multiple peaks	Apr-Jun & Oct-Nov	
R. mucronata	Natural	Jan-Feb & Dec	Mar-May	multiple peaks	Feb & May	(Wang'ondu 2009)
	Replanted	Jan-Apr & Nov-Dec	Sept	Oct- Nov	multiple peaks	(Wang'ondu 2009)
	Control	Feb-Apr & Aug-Oct	Mar	May & Nov	multiple peaks	This study
	15 cm silted	Feb-Jun & Aug-Dec	Mar-Apr & Sept-Nov	Mar-May & Nov-Dec	multiple peaks	
	30 cm silted	Feb-Apr & Aug-Oct	Mar-Apr	Mar-May & Nov-Dec	multiple peaks	
	45 cm silted	Feb-Apr & Sept-Oct	Mar-Apr	May & Nov	multiple peaks	

No information was available on phenological dynamics of *C. tagal* from the same site as the study area

In *A. marina*, the partially buried trees had peak flowering and fruiting earlier than those in the control while the highest partially buried *R. mucronata* trees fruited later into the experimental period than the controls and the 15 cm and 30 cm silted trees (Table 5.3).

A Kruskal-Wallis analysis showed a significant effect of sedimentation level on fecundity in *A. marina* ($H= 36.76$, $p < 0.001$). The highest flowering success was observed in the 45 cm partially buried trees (Table 5.2). However, the highest fruiting success was in the 30 cm sedimentation level as more flowers were aborted in the 45 cm sedimentation level (Table 5.2) A post-hoc multiple comparison of mean ranks revealed a significantly lower fruiting success in the controls as compared to all the sedimentation levels ($p < 0.05$). Fecundity variation in *C. tagal* had no observable trend with respect to sedimentation (Table 5.2) while *R. mucronata* had significantly higher flowering and fruiting success in the 15 cm sedimentation level ($p < 0.01$) than the control. However, above this level of sedimentation reproduction did not differ significantly from the controls and each other ($p > 0.05$). There were high rates of abortion as most of the young propagules produced dropped before maturity in all the plots.

Litter production rates (g DW m^{-2} $month^{-1}$) were highest in the 15 cm silted trees. When corrected for the number of trees per plot, the results showed a general higher leaf and reproductive litter production in the partially buried trees as compared to the controls. Production of these two forms of litter was highest with minimal sedimentation (15 cm) after which a reduction was observed, values that were still higher than the controls (Table 5.4). Litter production with woody material was however lower in the 15 cm silted plots than the other more silted (30 and 45 cm) ones.

Table 5.4 Mean (± SE) monthly litter fall in *Rhizophora mucronata* trees exposed to sediment burial simulating three levels of sedimentation (15, 30, 45 cm) over a one year period (November 2011 to November 2012) calculated at plot and individual tree level.

		Litterfall (g DW m^{-2} $month^{-1}$)		
	Treatment	**Leaves**	**Woody material**	**Reproductive parts**
At plot level	Control	75.77 ± 11.09	0.07 ± 0.04	1.15 ± 0.39
	15 cm	79.68 ± 15.08	0.12 ± 0.08	4.67 ± 1.44
	30 cm	67.12 ± 10.84	2.79 ± 2.46	3.76 ± 1.94
	45 cm	47.76 ± 9.27	2.42 ± 2.00	2.91 ± 1.94
At tree level	Control	18.94 ± 2.77	0.02 ± 0.01	0.29 ± 0.10
	15 cm	39.84 ± 7.54*	0.06 ± 0.04	2.34 ± 0.72
	30 cm	33.56 ± 5.42	1.39 ± 1.23	1.88 ± 0.97
	45 cm	23.88 ± 4.63	1.21 ± 1.00	1.46 ± 0.97

*Marked value is significantly different from control at $p < 0.05$

5.4 Discussion

Higher rate of leaf flushing observed in the partially buried *A. marina* and *C. tagal* in this study is in contradiction with our expectations of stress-induced mortality as a result of increased sedimentation as also expressed by Terrados *et al*. (1997) and Ellison (1998). This could be attributed to the 'advantages' associated with terrestrial sediment input such as nutrients influx (Alongi *et al.*, 2005; Lovelock *et al.*, 2010) and greater bacterial mineralization associated with increased sediment input as suggested by Lovelock *et al*. (2007). This in turn resulted in the observed increased rate of leaf flushing which is also in tandem with observations made by Lovelock *et al*. (2006b) in fertilised *R. mangle*. Nevertheless it was striking that the 'advantages' of sedimentation in *A. marina* were only expressed during the wet season. Though not systematically established in this study, the fact that higher inundation classes are less frequently inundated and therefore trees growing here highly depend on rain water to make new biomass could partly explain the observation in *A. marina*. Additional sediment load through sedimentation raises the height above datum with relatively high minimum salinity (Appendix S2) making the trees even more dependent on rain water thus explaining the high leaf gain during the wet season and reduced gain during dry season.

Despite the leaf flushing rates differing among treatments, the timings are comparable to those obtained in a natural landward *A. marina* site (similar inundation class as the current study) and reforested sites in a study conducted in Gazi Bay in the past (Wang'ondu, 2010 and shown in Table 5.4). *R. mucronata* leaf flushing patterns were also similar to results obtained earlier by Wang'ondu (2009) in Gazi Bay. Such multimodal peaked patterns in the congeners of the species of this study have also been observed elsewhere (Wium-Anderson, 1981; Coupland *et al.*, 2005). As such, the results in this experiment demonstrated that sedimentation does not affect the ever-growing nature of this species at least in the first year of partial burial.

Increased leaf loss in *C. tagal* and low replacement rate in partially buried trees which was even higher in 45 cm silted trees is an indicator of the onset of inhibitory responses in the trees due to sedimentation at this level. However, the fact that all partially buried trees showed either increased leaf production or leaf replacement rates similar to the controls after the second quarter (six months in to the experiment), suggests the ability to adapt to sedimentation. Moreover, leaf loss in the 45 cm treatment also decreased significantly indicating possibilities of acclimatization. Leaf loss is part of the normal productivity cycle of an ecosystem (Zalamea and Gonzalez, 2008) and although the rates cannot be pegged directly on sedimentation, the progressive increased rates in *C. tagal* could be a manifestation of stress. *C. tagal* therefore seemed to be the most sensitive to partial burial among the three study species. Additionally, *C. tagal* have been found to bear long lived leaves (Wium-Andersen and Christensen, 1978) and the contrary findings in this study are indicators of stress imposed by the sedimentation. There has been evidence of the negative effect of drought on leaf longevity (Mulkey *et al.*, 1991, 1993), suggesting a possibility of physiological drought induced by sedimentation. However, under sedimentation the species with longer leaf longevity are the most affected unlike under drought conditions (Mulkey *et al*. 1993; Wium-Andersen and Christensen, 1978). Leaf flushing pattern was nevertheless not influenced by partial burial as the trees showed a bimodal leaf flushing pattern characteristic of the species when growing in frequently inundated sites (Wium-Andersen and Christensen, 1978).

Increased leaf area which was observed with sedimentation for all the species is in coherence with studies on mangrove growth in the New Zealand estuary (Lovelock *et al.*, 2007). In that study, higher leaf area index was observed in sites receiving larger loads of sediment as compared to the less silted ones. Increase in leaf area may in turn lead to increased total photosynthesis (Reich *et al.*, 1998) which could probably explain the increased shoot elongation observed in *A. marina* and *R. mucronata* with sedimentation. The possible increased hypoxic conditions that can be caused by an increased barrier for oxygen exchange reaching the root zones as a result of sedimentation might have been counteracted by crab burrows observed in the plots (Plate 5.1c). Such crab burrowing activities has been shown to aid in aeration of the sediment (Smith *et al.*, 2009). Additionally, crab burrowing has also been observed to help maintain relatively low levels of salinity and their exclusion led to increased interstitial salinity in a restored coastal marsh in Florida (Smith *et al.*, 2009). Nevertheless, above the 30 cm sedimentation level, *A. marina* and *R. mucronata* leaf area began to decline indicating attainment of a threshold. Moreover, in *C. tagal* the leaf sizes at 45 cm were lower than the control indicating an inhibitory response as a result of increased levels of partial burial.

Succulence values obtained in this study are within the range of those obtained by Wang *et al*. (2010) in the same species indicating no increased water or nutrient stress induced by sedimentation. Succulence is a characteristic feature of xerophytes associated with water and/or nutrient conservation as well as protection against light and herbivory (Choong *et al.*, 1992). Since mangrove trees also suffer from physiological drought (as a result of the highly saline environment), they store desalinated water. As such, they are more succulent than their neighbours, the mangrove associate (Longstreth and Nobel, 1979; Wang *et al.*, 2010) or terrestrial species, and conserve nutrients (Feller, 1996; Saenger, 2002). A shift in timing of the reproduction pattern (between controls and silted trees) was not observed in *C. tagal* (Table 5.4). In the other species where there was some degree of shift, the timings were still more or less in concurrence with those obtained in an earlier study in the same site (Table 5.4). Although unfavourable growth conditions may result in significant shifts in reproduction timing (Fitter and Fitter, 2002) the results show no such link. Moreover, sedimentation was noted to improve fecundity in all the studied species.

5.5 Conclusion

Large sedimentation events may not affect timing of phenological events but rather influence rates. This is species and site-specific but there is a general trend towards increased leaf emergence, reproduction, shoot growth and productivity at relatively shallower partial burial. Further and irrespective of the sedimentation level, if such partial burial depths are maintained at a stable level over a long period of time, the trees are able to acclimatise thereby maintaining the phenological dynamics characteristic of unaffected trees. The results show that while large sedimentation events may negatively affect tree development and productivity, mangroves acclimatise to partial burial capitalising on advantages of accretion and thus ensure an even better growth. Instantaneous large input of sediment into the mangrove ecosystems as envisaged by climate change impacts may therefore not affect the phenological cycle of the studied mangrove tree species negatively but rather positively unless selected thresholds are exceeded above which growth and productivity declines.

CHAPTER 6:

Partially buried mangrove trees ensure continued hydraulic conductivity through adjustment in xylem structure.

Submitted to the journal of Plant and Soil

Abstract

Background and aims: Whereas natural sedimentation may not affect mangrove trees adversely, large and sometimes episodic delivery of sediment may result in decreased growth, dieback or mortality. In this study, we aim at understanding the effects of different levels of partial sediment burial on mangrove tree anatomical structure and function.

Methods: Trees of *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata* were experimentally buried with terrestrial sediment to simulate different sedimentation levels (15, 30 and 45 cm). After 14 months, branch hydraulic conductivity, xylem structure and stomatal properties were assessed.

Results: All 15 and 30 cm partially buried trees had higher hydraulic conductivity, while the 45 cm buried trees showed values comparable to the controls. Vessel grouping, vessel lumen size and potential conductive area varied considerably with burial level and among species. Stomatal adjustment was observed in *C. tagal* with 20.9-36.7% reduction of total stomata area in buried trees.

Conclusions: Sedimentation appears to result in changes in vessel and stomatal properties of partially buried mangrove trees after relatively short period of exposure, traits which may be important in ensuring hydraulic conductivity.

Contributors: Okello J.A.- main author; Schmitz N.- experimental design; Copini P.- write-up; Hans Beeckman- co-promoter; Dahdouh-Guebas- supervision; Kairo J.- experimental design, Koedam N.- lead promoter, experimental design and supervision; Robert E.M.R.- write up

6.1 Introduction

Water availability to a plant reflects the ease with which a plant can extract water from the soil (Van Liera, 2014). It may thus be a function of many factors including and not limited to, drought, frost, flooding, soil characteristics such as texture and structure as well as salinity as in the case with mangroves. Sedimentation in mangroves may result in low water availability occasioned by increased difficulty in root water absorption (Tomlinson, 1994). This may be due to increased compaction which reduces sediment pore sizes and thereby requires greater tension to extract water from the soil (Sperry *et al.*, 1998). Additionally, sedimentation may lead to increased hypoxia in the sediment (Thrush *et al.*, 2004), conditions which could lead to increased physiological drought as water channel proteins (aquaporins) are downregulated by hypoxia (Laur and Hacke, 2014) and as such may equally result in decreased water uptake by the roots (Herrera, 2013). Conversely, and though it may not be the case with mangroves since they do not develop deep rooting systems, it has been observed that aquaporin activity may be upregulated during severe drought resulting in increased deep root hydraulic conductivity (Johnson *et al.*, 2014). The impacts of decreased water uptake as a result of sedimentation can also be equated to physiological drought and its consequential increased negative xylem sap resulting in embolism and its propagation among functional vessels (Lens *et al.*, 2013). Embolism in turn has a possible effect on reduction in hydraulic conductivity, K (Hacke, 2014; Ladjal *et al.*, 2005) but reduced K may also be directly associated with the increased negative xylem pressure (Hacke, 2014).

According to the air seeding theory, cavitation occurs when air (which is mainly from the fibres or from an adjacent air-filled conduit) is drawn into the water-filled conduit through pores on the cell wall (Sperry and Tyree, 1988). The pores create an air-water meniscus which eventually breaks off when the difference between air pressure (Pa) and xylem pressure (P_X) exceeds a critical pressure difference (Plavcova *et al.*, 2011). Other than the trigger from gas bubble introduction in to a functional vessel, cavitation can also be initiated by weak adhesion in the water-conduit wall boundaries resulting in the breakage of a water column (Lens *et al.*, 2013). Once inside the vessel, the nano-bubble will expand to fill the vessel but this again can only occur when the bubble is above a certain critical radius (Schenk *et al.*, 2015). With the fact that most plants experience xylem pressures (Px) that are close to the threshold for xylem cavitation (Tyree and Sperry, 1988), cavitation may occur merely due to atmospheric moisture fluctuations resulting from transpiration-induced loss of equilibrium within a time scale of a day (Meinzer *et al.*, 2009). However, extreme conditions such as low water availability have been implicated in most literature as the major cause of loss of conductive area in trees (e.g. Awad *et al*., 2010; Ball *et al*., 2006; McDowell *et al*., 2008).

In the case of reduced water uptake by the roots, there may be a tendency of a shift in xylem characteristics towards ensuring safety against cavitation rather than efficiency in sapflow hence the trees experience decreased hydraulic conductivity (de Silva *et al*., 2012).

In response to reduced water uptake capacity, plants tend to display a shift in xylem characteristics towards ensuring safety against cavitation rather than efficiency in sapflow (de Silva, 2012). For instance, tree species growing in xeric environments tend to show higher vessel grouping as compared to those under mesic conditions (Carlquist, 1984). This trait has been found to be one of the most informative in explaining interspecific variation in 50% loss of conductivity, P_{50} (Scholz *et al*., 2013). In mangroves, trees growing under higher salinity conditions form relatively narrower conduits that are often more clustered and are of higher density (Robert *et al*., 2009a; Schmitz, 2006). Such safety characteristics can either (i) reduce chances of cavitation and consequent expansion of the nano-bubble to fill the entire vessel by minimising hydraulic resistance (Christman and Sperry, 2010; Jansen *et al*., 2009; Jansen *et al*., 2011), or (ii) reverse or repair embolism through refilling of air-filled vessels from neighbouring cells (Brodersen *et al*., 2010; Hacke and Sperry, 2003; Tyree *et al*., 1999). Further, trees reduce its impacts through sacrificing distal organs such as twigs and branches tips (Rood *et al*., 2000; Sperry and Pockman, 1993). Leaves can also help to minimise hydraulic failure by regulating transpiration rates (Meinzer and Grantz, 1990; Wang *et al*., 1992) through maximisation of stomatal conductance while preventing critically negative xylem pressure (Jones and Sutherland, 1991; Meinzer and Grantz, 1990; Tyree and Sperry, 1988).

Various effects of sedimentation have been previously documented including: reduced growth and survival of mangrove tree seedlings (Terrados *et al*., 1997; Thampanya *et al*., 2002); as well as premature fruiting (Mohamed, 2008). Loss of productivity and dieback of mature mangrove stands have also been reported after large and sudden sedimentation events of 5 to 200 cm in different locations around the globe (Ellison, 1998). The current study simulates the occurrence of large and sometimes episodic delivery of sediment in an experimental set-up involving three mangrove tree species (*Avicennia marina* (FORSSK.) VIERH, *Ceriops tagal* (PERR.) C.B. ROB and *Rhizophora mucronata* LAM.), commonly found along the Kenyan coast and generally in the Indo-West Pacific region (Tomlinson 1994) we investigate the impacts of such events on hydraulic conductivity, xylem structure and stomatal properties of these tree species. It is hypothesised that large sedimentation events, (i) lead to increased hypoxia in sediment, (ii) reduce hydraulic conductivity in partially buried trees and (iii) initiate development of adaptive features in stomatal properties and xylem characteristics upon burial. This study is intended to provide information on the ability of mangrove trees to cope with large sedimentation events within their habitat and hence to contribute to the assessment of resilience of mangrove forests to climate change impacts.

.

6.2 Materials and methods

6.2.1 *Study site and experimental set-up*

The field experiment was set up in plantations of *C. tagal*, *R. mucronata* and *A. marina* planted in 1994, 1998 and 2001 respectively in Gazi Bay, Kenya (4º22′S, 39º30′E). This section of the study was based in the same site and within the experimental plots described in Chapter 5 (see also Figure 6.1a, b).

The establishment was done in 2010 (*C. tagal*) and 2011 (*A. marina* and *R. mucronata*), and all plots were left to undergo full influence of natural mangrove processes (litter accumulation, natural regeneration and tidal influence).

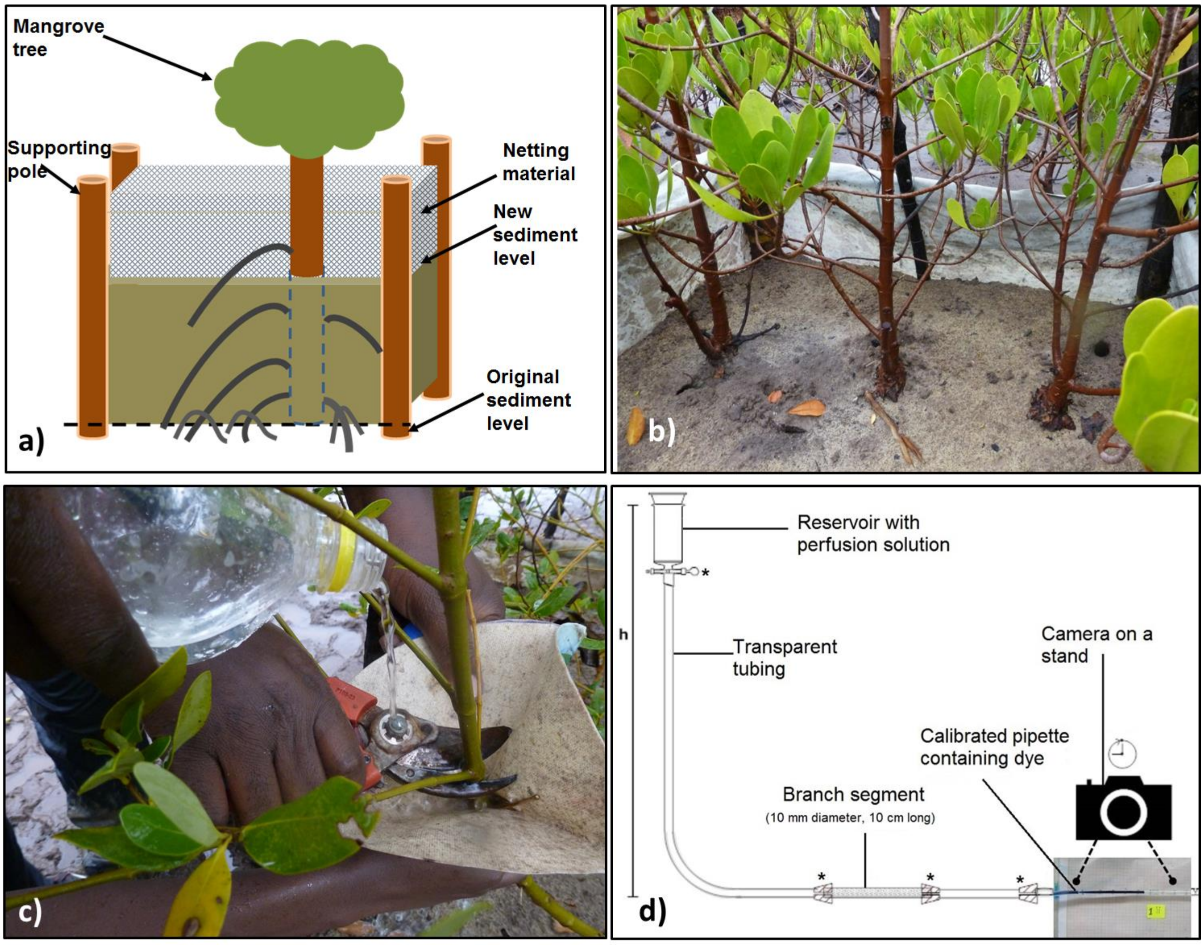


Figure 6.1 (a) Setup of the field experiment in which a mangrove tree is partially buried with terrestrial sediment from adjacent upstream areas; **(b)** *Ceriops tagal* trees in a section of one of the 30 cm sedimentation plots; **(c)** water being poured in to a funnel shaped plastic table mat held around a selected branch before cutting; **(d)** Laboratory set-up for hydraulic conductivity measurements. A camera is focused above a calibrated pipette laid on a graduated sheet of paper to take a series of pictures at regular intervals. h: the height of the reservoir (60-70 cm) that generates the pressure head, *: taps to start or stop flow of the perfusion solution within the tubing system. Adapted from Choat *et al*. (2011) and De Deurwaerder *et al*. (2016).

6.2.2 *Structural attributes*

Each plot had a varying number of trees that were 1.1 to 4.7 m high (Appendix I Table S3). Stem diameter for *A. marina* and *C. tagal* species was measured at 30 cm (D_{30cm}) since the trees were shorter and could not allow for the conventional diameter measurement at 130 cm (diameter at breast height or D_{130cm} *sensu* Brokaw & Thompson 2000). For *R. mucronata* diameter at breast height or 30 cm above the highest prop root was taken. The diameter range was 1.4-2.1 cm in *A. marina*, 4 – 6.3 cm in *C. tagal* and 11.4 – 15.5 cm in *R. mucronata* (Appendix I Table S3). The sediment which was applied covered the aerial roots to different extents among the – studied species, with a complete coverage in all burial treatments for *C. tagal* (Appendix I Table S3).

6.2.3 *Environmental variables*

Environmental variables including salinity, sediment nutrient content, height above datum and redox potentials were measured three months after setting up the experiment. Repeated salinity measurements were made monthly for another three months and redox potential was redone after six months. Interstitial water was collected using a punctured plastic tube connected to a vacuum pump and salinity measurements were done with a hand-held refractometer (ATAGO, Tokyo, Japan). Redox measurements were done using a portable pH/ORP (oxidation/ redox potential) meter with ATC (Automatic Temperature Compensation) and hold feature (HI 8424, Hanna instruments, USA). For both salinity and soil redox potentials, measurements were done by coring at 5 cm depth then after every 10 cm up to the 10 cm layer just below the original (below zero) sediment level in each of the treatments. Sediment nutrient analysis was done for three sediment cores collected up to 30 cm depth from terrestrial source and in the control plots using standard procedures described by APHA (1998) and Parsons (1984).

6.2.4 *Hydraulic conductivity measurements*

For the measurements of hydraulic conductivity, three branch samples from three trees of each experimental plot (one branch per tree; 16 plots; N=48) were collected after 14 months of exposure. Only trees that experienced minimal edge effect were considered for sampling (Appendix I Table S3). While the choice of branches was aselect, deliberate attempts were made to (i) ensure that they were from approximately the same position in the tree crown (height above ground level) and (ii) obtain samples with no or as few nodes as possible and with a diameter of 10 mm. Native branch hydraulic conductivity (K_h) was measured from 10 cm long segments of branches for *C. tagal* in June 2012, *A. marina* in July 2012 and *R. mucronata* in January 2013. The branches were cut at least 15 cm from the target branch segment during the morning of the day of measurement. This was done under water with the help of a funnel-shaped plastic table mat wrapped around the branch (Figure 6.1c). The branches were transported to the laboratory in a bucket with the cut tips touching onto a dump rug and the foliage covered with an opaque bag to minimise transpiration.

The sampled branches were then recut under water (Hao *et al.*, 2009) into segments of about 10 cm long. Where appropriate length without nodes could not be obtained, the side branch was carefully cut off and the exposed surface immediately sealed with parafilm to avoid water loss. Hydraulic conductivity was measured using the set-up depicted in Figure 6.1d

(Choat *et al.*, 2011). Perfusion solution used was 1.0% seawater, filtered through 0.2 µm Millipore syringe filters (Millex GS filter, Millipore Corrigtwohill Co, Cork, Ireland). This solution is similar to the ionic concentration of the sap within a mangrove stem (Scholander *et al.*, 1966; Ball, 1988; Choat *et al.*, 2011).

The hydraulic pressure for the water flowing through the branch segments was generated by a reservoir raised at 60 to 70 cm (Figure 6.1d) producing a constant pressure of 5.91 to 6.5 kPa. The flow rate through the branch segment was determined by tracking the motion of dye through a calibrated pipette (0.01/0.1 mm) connected to the distal end of the branch segment and laid on a grid paper. This was recorded at intervals of 15 to 30 seconds over 5 minutes (Figure 6.1d). The images were loaded in ImageJ (1.45s, Wayne Rasband, National Institute of Health, USA) and motion distances of the dye were measured to calculate sap flow rate. Native hydraulic conductivity (K_h) was then calculated as:

$$K_h = \frac{F \times L}{\Psi} = [\frac{m^3 s^{-1} * m}{MPa}] = [m^4 s^{-1} MPa^{-1}] \qquad \textbf{(1)}$$

where F is flow rate [m^3 s^{-1}], L is length of the branch segment [m] and Ψ is applied pressure [MPa]. Considering that 1 m^3=1000 kg; we express the units as kg $m^{-1}s^{-1}MPa^{-1}$

Leaf areas of all leaves (A_L) from the distal end of the branch segment were measured using a Portable laser leaf area meter (CI-202, CID Bio-science, Washington, USA). The average leaf area was then used to calculate leaf-specific hydraulic conductivity (K_L) as defined in Zotz *et al*. (1997):

$$K_L = K_h/A_L \ [\text{kg } m^{-1}s^{-1}MPa^{-1}] \qquad \textbf{(2)}$$

where A_L is the total leaf area on a given experimental branch segment.

Small discs (*ca.* 1 cm long) were cut from each branch segment and the transverse section trimmed using a sledge microtome (GSL1-microtome, Zürich, Switzerland, Gärtner *et al.*, 2014). The discs were then photographed using a camera (Olympus N547, Tokyo, Japan) attached to a stereo microscope (Olympus SZH10, Tokyo, Japan) after which the xylem tissue proportions were measured using ImageJ (1.45s, Wayne Rasband, National Institute of Health, USA). The mean xylem area was then used to adjust native hydraulic conductivity to obtain xylem-specific hydraulic conductivity (K_S) as defined in Zotz *et al.* (1997) and Lopez-Portillo *et al.* (2005).

$$K_S = K_h/A_X \ [\mathrm{kg\ m^{-1}\ s^{-1}\ MPa^{-1}}] \tag{3}$$

where Ax is the mean xylem area.

6.2.5 *Xylem structure measurements*

Transverse sections of 20 µm thickness were made from each of wood samples (cut from the branch segments used for hydraulic conductivity) by use of a sledge microtome (GSL1-microtome, Zürich, Switzerland, Gärtner *et al.*, 2014) after which they were stained with a safranin-alcian blue mixture. Vessel characteristics (vessel density, vessel diameters and vessel grouping) were determined in six fields of view of about 0.385 mm² or 0.239 mm² in each of the two transverse sections (two per sample). The fields were set as close to the bark as possible (within 700 – 1000 µm from the bark) to reduce chances of including wood formed before the experimental period. Making use of the image-acquisition and archiving software CellB (Olympus Cell^B Soft Imaging System GmbH, Münster, Germany), the short and long vessel axes (a, b) were measured for 20 vessels per field of view (in total, 120 per sample and 360 per treatment). All vessels in the same fields of views were then counted (20 – 160) and categorized according to the number of vessels per vessel group (two's three's, four's and more than four). The vessel lumen area and potential conductive area ($A_{conductive}$) were calculated using equation 4 and 5 respectively.

$$A_{vessel} = \pi\left(\frac{a}{2} * \frac{b}{2}\right) \tag{4}$$

$$A_{conductive} = A_{vessel} \times \text{vessel density} \tag{5}$$

where, a and b are the short and long vessel axes, A_{vessel} is the vessel lumen area

Equivalent vessel diameter (De, equation 6; Lewis, 1992) was calculated to enable comparison of vessels with diverse cross-sectional shapes.

$$De = \sqrt{\frac{2a^2\,b^2}{a^2 + b^2}} \tag{6}$$

The degree of vessel grouping was quantified based on vessel grouping index as described by Carlquist (2001), i.e. the total number of vessels divided by total number of vessel groups.

6.2.6 *Stomata measurements*

The third pair of leaves (counted from the shoot tip) was collected from all branches used for the determination of hydraulic conductivity. Stomatal imprints of 1-2 cm^2 in size were made mid length and close to the mid rib from the abaxial surface of each leaf of *C. tagal* and *R. mucronata* (Gitz and Baker, 2009). For *A. marina* leaves, macerations were prepared according to Yeung (1998), using 1-2 cm^2 pieces of leaves cut from the same position as the other species. All the stomata were counted and lengths and widths of guard cells of 15 closed stomata were measured in three different fields of view (0.4 mm^2) using the image-acquisition and archiving software CellB (Olympus $Cell^B$ Soft Imaging System GmbH, Münster, Germany), via an Olympus UC30 camera fitted on an Olympus BX60 microscope (Wisconsin-Madison, USA). Total stomatal area was calculated by multiplying stomata density (count per unit leaf area) by median stomatal area.

6.2.7 *Statistical analysis*

Data analysis was performed in STATISTICA 7.0 (StatSoft Inc., Tulsa, USA) applying a significance level of 0.05. Each tree selected per plot was considered as a replicate of the other. Main-effects ANOVA was used to test for differences in soil redox potential across treatments and among the species. One-way ANOVA was used to test for differences in conductivity, xylem structure and stomata properties across the treatments. Where assumptions for parametric testing were not met even after transformation, the non-parametric Kruskal-Wallis test was used to compare various variables across the different levels of partial burial. The landward and seaward plots of *C. tagal* were treated separately except for potential conductive area and total stomatal area where there was no significant difference between the two. Spearman's Rank correlation was used to test for relationship between vessel grouping index and hydraulic conductivity.

6.3 Results

The results of this section of the study were obtained against a background of survival of trees of all the studied tree species, except for *C. tagal* of which a few trees (five out of the 17 trees in the 45 cm burial treatment) died within the first six months after burial (Chapter 6).

6.3.1 *Environmental variables*

Redox potential values were within the ranges associated with higher inundation classes in mangroves (Matthijs *et al*., 1999) ranging between -4 to 305 mV in the *A. marina* plots and between -44 and 20 mV in the *C. tagal* and *R. mucronata* plots. However, the maximum redox potential values obtained in *A. marina* (recorded in the control) surpassed the scale by Matthijs *et al*. (1999). Further, we did not find significant difference among the treatment levels (F=0.75, p>0.05), but the soil redox potential values were more negative in the plots of higher sedimentation treatments particularly for *C. tagal* and *R. mucronata* (Figure 6.2). Values obtained in the *C. tagal* and *R. mucronata* plots were significantly different from those recorded in *A. marina* plots (F=35.25, p<0.05).

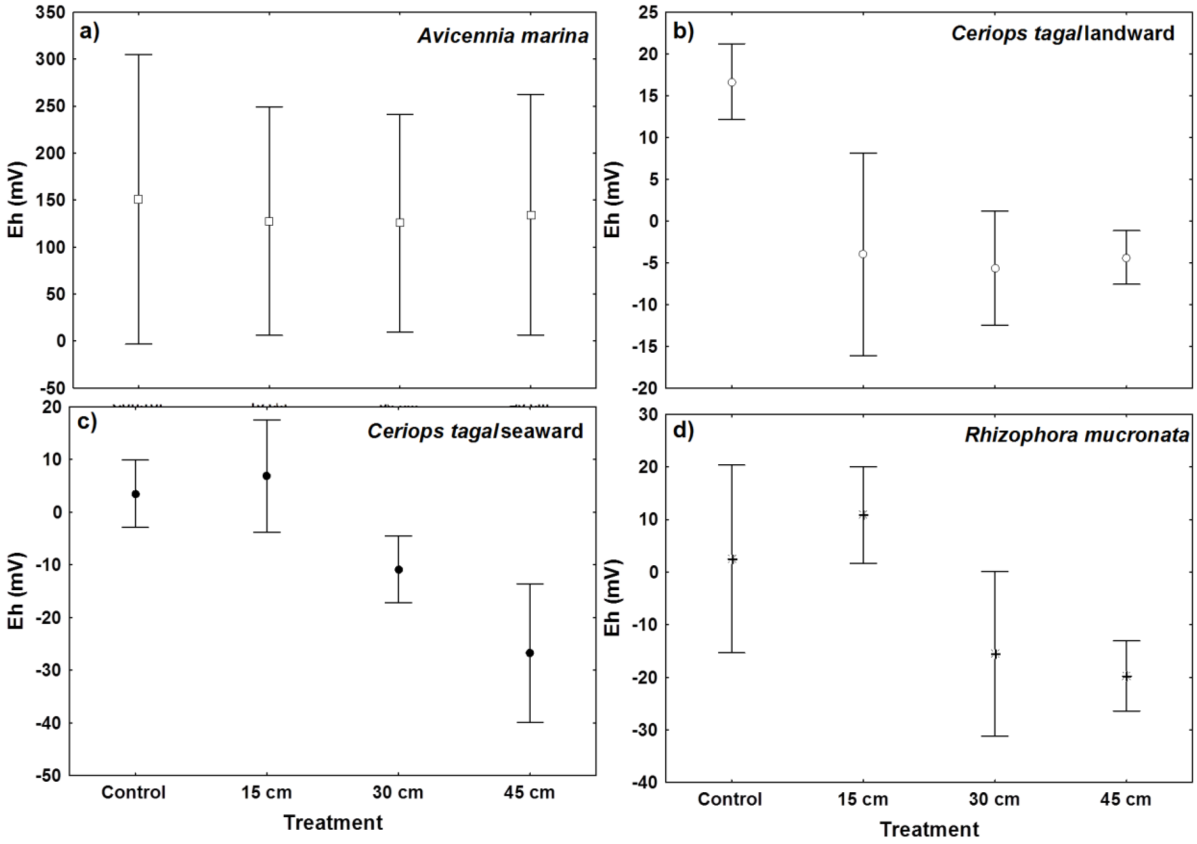


Figure 6.2 Soil redox potential (mV) measured at different sediment depths (5 cm then after every 10 cm including 10 cm below original sediment level) in (a) *Avicennia marina*, (b) *Ceriops tagal* from landward plots (c) *Ceriops tagal* seaward (d) *Rhizophora mucronata*. Plots: marker (mean), whisker (±SD). Measurements were done 3 months and six months after partial burial.

There was no systematic trend recorded in salinity ranges with sedimentation for *A. marina* and *C. tagal*. In *R. mucronata* the salinity range increased in the order 14‰, 17‰, 22‰, 27‰ with each sedimentation level (Appendix I Table S4). This was also linked to progressive increase of height above datum with sedimentation from control 3.09 m; 15 cm–

3.31 m; 30 cm– 3.34 m; and 45 cm– 3.52 m. The minimum salinity recorded in the 15 and 30 cm sedimentation treatments (*C. tagal*) was much lower as compared to salinity values in the control plot. Sediment nutrient analysis revealed higher phosphate, nitrate and ammonia levels in the terrestrial sediment as compared to sediment from the controls (Appendix I Table S4).

6.3.2 *Hydraulic conductivity*

Except for *C. tagal* in the seaward plots, increased hydraulic conductivity (K_L and K_S) was observed with 15 and 30 cm sediment burial while at 45 cm, it was comparable to the controls (*A. marina* and *C. tagal*; Figure 6.3a, b, c and d) or slightly higher (*R. mucronata*; Figure 6.3g and h).

A. marina showed the highest hydraulic conductivity in 15 cm burial level (Figure 6.3a and b) with both 15 and 30 cm treatments having significantly higher K_L ($H=36.74$, $p<0.001$, Figure 6.3a) and Ks ($H=26.69$, $p<0.001$, Figure 6.3b) compared to the controls.

C. tagal landward treatments showed different hydraulic conductivity trends from the seaward treatments, which are in longer and higher flooding regimes. In the branches from the landward plots, K_L was significantly higher in the 15 and 30 cm sediment burial levels as compared to the rest of the treatments ($H=52.78$, $p<0.001$). Branches from the highest sedimentation level (45 cm) showed similar K_L as the controls (Figure 6.3c). Ks followed a similar pattern with a significantly higher conductivity in the 15 cm level than the control (Figure 6.3d). K_L was significantly higher in the 30 cm burial treatment as compared to the rest of the treatments ($H=54.75$, $p<0.01$; Figure 6.3e). Branches from trees in the 30 cm and 45 cm burial treatments had significantly higher Ks than the controls and those from the 15 cm burial level ($H=43.16$, $p<0.00$).

Hydraulic conductivity in *R. mucronata* was highest in the minimum burial treatment (Figure 6.3g and h). Both K_L and Ks were significantly higher in branches from the partially buried trees compared to the controls (K_L: $H=60.51$, $p<0.001$ Figure 3g; Ks: $H=52.49$, $p<0.001$, Figure 6.3h).

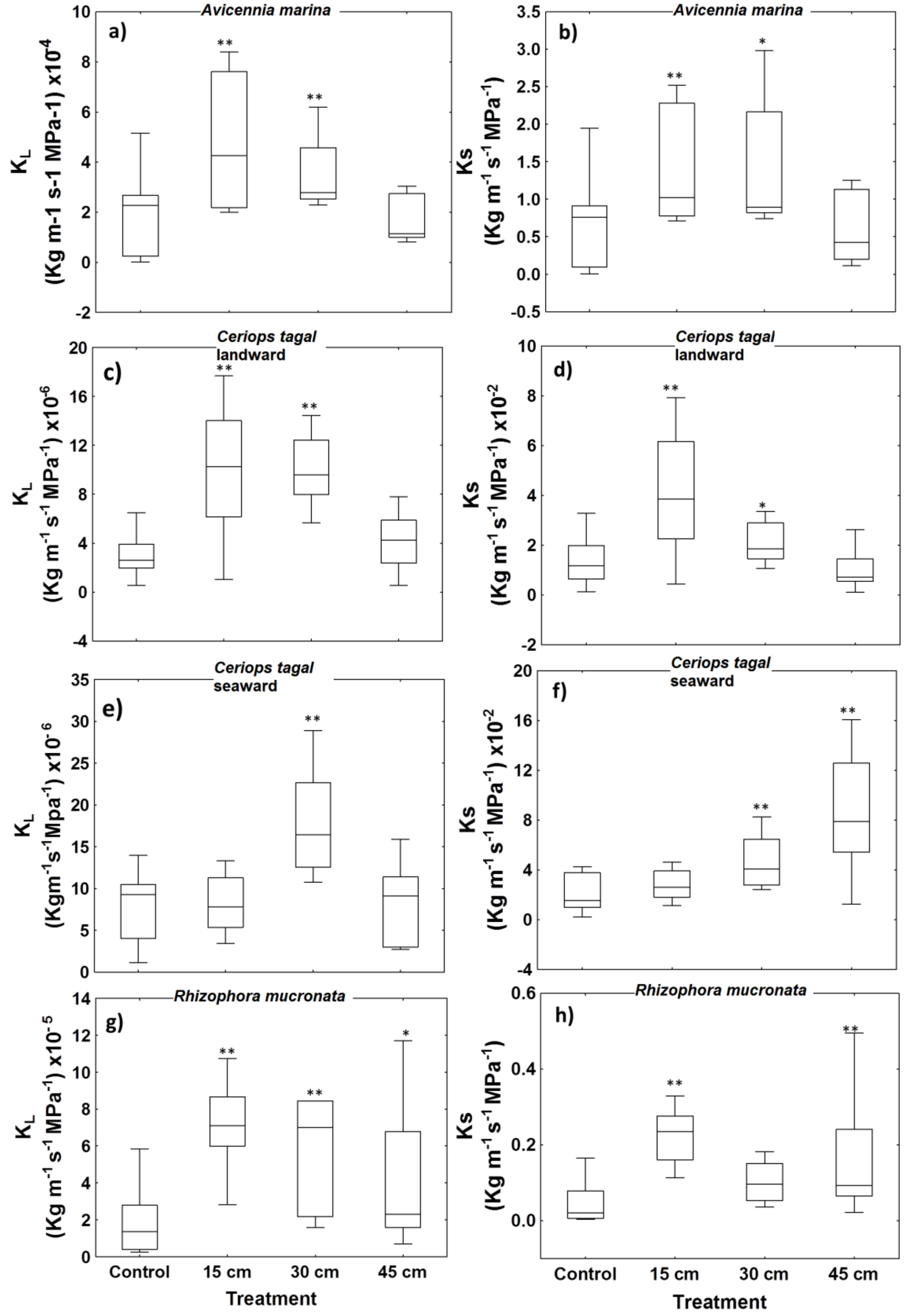


Figure 6.3 Branch hydraulic conductivity, standardized for total branch leaf area (K_L; **a, c, e & g**) and for xylem area (Ks; **b, d, f & h**) of the three studied species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*) after 14 months of experimental sediment burial simulating three sedimentation levels (15, 30 and 45 cm). The bars marked with an * and ** are respectively significantly ($p<0.05$) and highly significantly ($p<0.01$) different from the control. Box plots: line (median), box (25–75%), whiskers (non-outlier range: range of values falling below the upper outlier limit and above the lower outlier).

6.3.3 *Wood anatomy and stomatal area*

Branches of *A. marina* from the 45 cm burial treatment had a combination of relatively higher De (Figure 6.4a) and a higher potential conductive area compared to the control (Table 6.1). However, these two features did not produce an increase in hydraulic conductivity at this level. The species showed the highest vessel grouping index in the 15 cm buried trees and the lowest at highest burial level (45 cm) (Figure 6.4b). This trend of vessel grouping index with burial was similar to the observed hydraulic conductivity (Figure 6.3a and b). The total stomatal area in *A. marina* however showed no distinct pattern with increasing sediment burial (Table 6.1).

Table 6.1 Vessel lumen area per unit xylem area (potential conductive area) and stomatal area per unit leaf area in the three studied mangrove tree species (*Avicennia marina, Ceriops tagal* and *Rhizophora mucronata*) exposed to partial sediment burial simulating three levels of sedimentation (15, 30 and 45 cm) for 14 months. N/s: not significantly different from the control (p>0.05); **C. tagal* from landward and seaward were not significantly different from each other.

Species	**Treatment**	**Vessel lumen area (μm^2/mm^2) x10^4**				**Total stomata area (μm^2/mm^2) x10^4**			
		Median	**Lower Q**	**Upper Q**	**p value**	**Median**	**Lower Q**	**Upper Q**	**p value**
A. marina	Control	6.59	6.30	7.10		3.55	2.93	3.87	
	15 cm	7.96	6.40	8.51	N/s	3.02	2.83	3.26	N/s
	30 cm	7.21	5.14	9.10		4.51	4.15	4.94	
	45 cm	8.45	6.43	11.14		3.18	2.36	4.14	
**C. tagal*	Control	7.08	5.38	7.56		6.03	5.04	6.46	
	15 cm	7.31	6.79	7.78	N/s	4.08	3.69	4.91	N/s
	30 cm	5.73	5.04	6.34		3.71	3.41	4.02	<0.01
	45 cm	6.79	4.80	7.89		4.74	3.67	5.46	N/s
R. mucronata	Control	4.76	3.60	5.73		8.75	8.15	9.28	
	15 cm	8.4	6.96	9.95	<0.01	8.77	8.48	8.94	N/s
	30 cm	10.14	8.25	10.85	<0.001	9.51	8.48	9.99	
	45 cm	5.62	4.99	7.54	N/s	9.45	8.49	10.38	

Partially buried *C. tagal* trees from landward plots had branches with narrower vessels (Figure 6.4c) as compared to the controls, dipping significantly at the 30 cm burial level (H=155.88, p<0.001). These trees (30 cm burial level) showed the highest vessel grouping index (Figure 6.4d). The branches from seaward plots differed from those from the landward plots showing a combination of significantly wider vessels and lower vessel grouping in partially buried trees as compared to the controls (Figure 6.4e and f). Vessel diameters were positively correlated with Ks (R=0.55, p<0.05) while vessel grouping index did not correlate with the hydraulic conductivity rates observed, Response in potential conductive area and stomatal properties were similar in the two tidal locations as both seaward and landward plots showed lower values in the partially buried trees as compared to the controls (Table 6.1).

In *R. mucronata*, De was significantly higher in the highest level of partial burial (45 cm, Figure 6.4g). The vessel grouping index increased with the level of sediment burial ($H=134.8$, $p<0.001$), reaching a maximum in the 30 cm burial treatment (Figure 6.4h). Although the vessel grouping pattern did not match the trend of the observed hydraulic conductivity (Figure 6.3g and h; Figure 6.4h), Spearman Rank-Order correlation revealed a positive correlation between vessel grouping index and Ks irrespective of sedimentation level ($R=0.61$, $p<0.05$). A multiple comparison of means showed that *R. mucronata* had a significantly higher potential conductive area with the relatively lower burial levels ($p<0.01$), peaking in the 30 cm burial treatment (Table 6.1). Stomatal area was relatively higher than the control in the leaves from the 30 and 45 cm burial level (Table 6.1) but none of the treatments differed significantly from the controls ($H=4.02$, $p>0.05$).

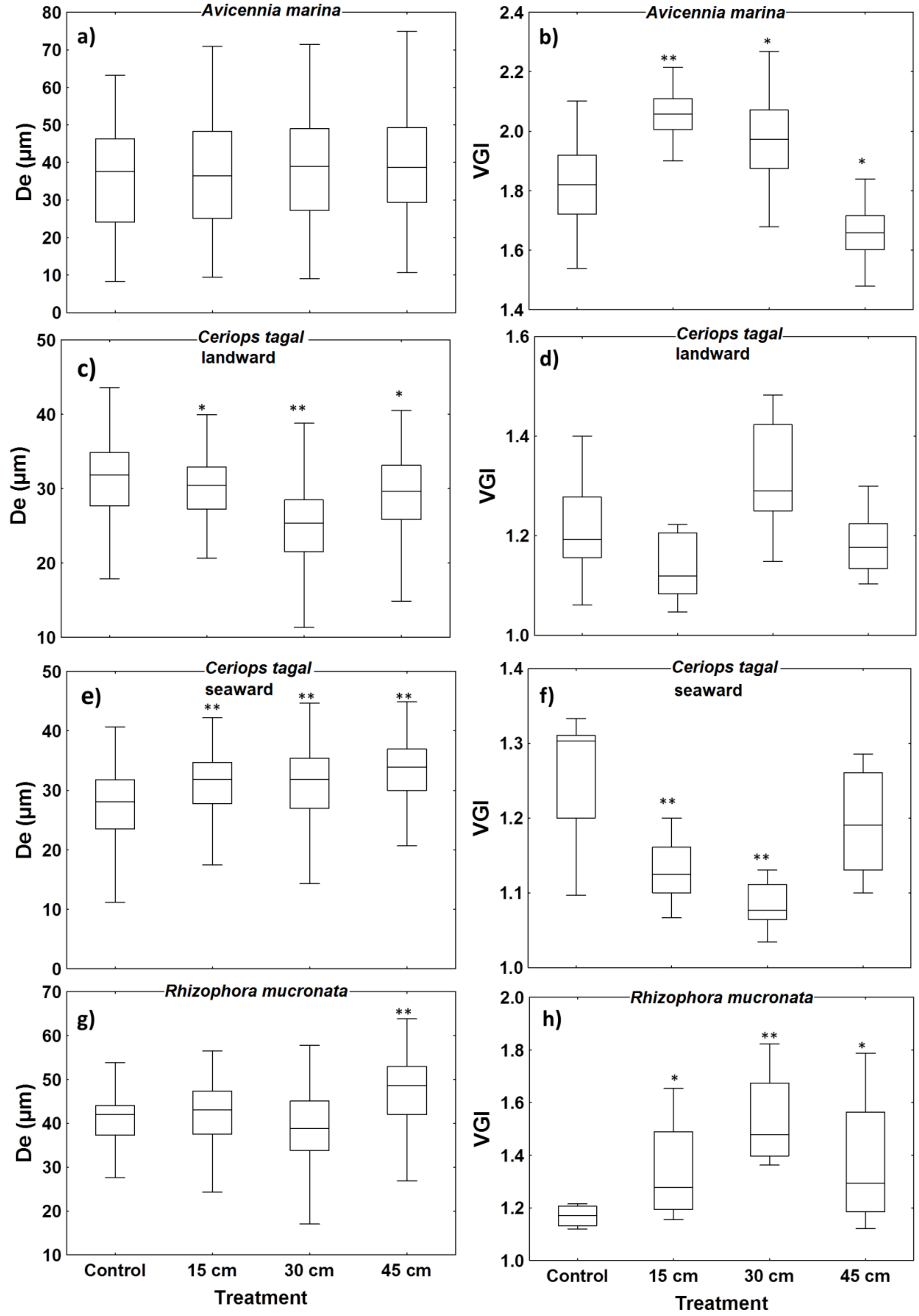


Figure 5 4 Equivalent vessel diameter (De**; a, c, e, g**) and vessel grouping index (VGI; **b, d, f, h**) in the three studied species (*Avicennia marina*, *Ceriops tagal*, and *Rhizophora mucronata)* after 14 months of exposure to experimental sediment burial simulating three levels of sedimentation (15, 30 and 45 cm). The bars marked with an * and ** are respectively significantly ($p<0.05$) and highly significantly ($p<0.01$) different from the control.

Box plots: line (median), box (25–75%), whiskers (non-outlier range: values falling below the upper outlier limit and above the lower outlier).

6.4 Discussion

6.4.1 *Large sedimentation events may increase hydraulic conductivity*

After 14 months of experimental burial, a higher hydraulic conductivity was observed for the 15 and 30 cm burial treatments in all three studied mangrove species and there was no significant reduction in hydraulic conductivity with respect to the control in the 45 cm burial treatment in any of the species (Figure 6.3). Despite the interspecific variations in hydraulic conductivity, also observed by Lovelock *et al*. (2006b) in samples from the Indian River lagoon and Twin Cays for different mangrove species, all three mangrove tree species we studied were able to ensure continued sap flow with sediment burial. Such interspecific differences can be attributed to anatomical variations among mangrove species including intervessel pit characteristics (Choat *et al*., 2007; Schmitz *et al*., 2008).

Other than interspecific variations in hydraulic conductivity, there was disparate response between landward and seaward *C. tagal* plots. Whereas in the landward plots there was a threshold above which conductivity decreased and became comparable to the control trees (Figure 6.3c and d), the seaward plots had increased conductivity (corrected for xylem area, Ks) reaching a maximum (2 fold of the control) at the highest sedimentation level (Figure 6.3f). Such variations can be linked to local differences in salinity fluctuations, nutrient availability and inundation durations within an intertidal area (Lovelock *et al*., 2006b; Robert *et al*., 2009b; Schmitz *et al*., 2006; Schmitz *et al*., 2007).

Water transport and hydraulic failure can play a significant role in regulating plant physiological responses at all levels (Mencuccini, 2003) and has been cited by McDowell *et al*. (2013) as a potential cause of tree mortality. A recent study by Rowland *et al*. (2015) has provided further evidence regarding drought related deaths of tropical trees triggered by hydraulic failure. However, the death of a few *C. tagal* trees observed for this experiment (Chapter 6) could not be automatically attributed to hydraulic failure. The results of this study instead suggest adaptive strategies in partially buried mangrove trees that might have resulted in the bell-shaped (*A. marina* and *R. mucronata*) or steady increase (*C. tagal*) pattern of hydraulic conductivity (Ks) with increasing sedimentation level.

While these findings show relative increase in hypoxia (more negative soil redox potential) as a result of sedimentation (Figure 6.2; Thrush *et al*., 2004), they do not provide sufficient evidence regarding a possible link with reduced hydraulic conductivity, at least not in a persisting way (Figure 6.3). Since sedimentation has at least partially the same effect as drought through reducing water uptake by the roots (Tomlinson, 1994; Sperry *et al*., 1998), it would be logical that this translates to decreased hydraulic conductivity through induction and spread of embolism in otherwise functional vessels (Lens, 2013). Moreover, embolism is the most important factor that impact on short-term whole plant hydraulic conductivity other than extracellular sapflow dynamics (Hacke, 2014). Drought in itself may also lead to acclimatisation through reduction in Ks and K_L mainly as a means to preserve the little available water (Ladjal *et al*., 2005). The observed increase in hydraulic conductivity suggests involvement of ion-mediated increase in Ks as has been elaborated by Hacke (2014) with possible embolism related to sedimentation. The bell shaped hydraulic conductance trend however indicate that further sedimentation (larger than 45 cm) could have negative effect on hydraulic conductivity. Further, the consistent K_L pattern observed in all the species also suggest an overriding influence of leaf area on stem hydraulic conductivity upon burial.

Other studies have shown that natural sedimentation promotes mangrove tree growth and expansion of mangrove forest (Furukawa and Wolanski, 1996; Lovelock *et al*., 2007) and that the process is associated with nutrient input (Alongi *et al*. 2005; Lovelock *et al*. 2010). We observed an increase in hydraulic conductivity at least at relatively lower burial treatments (15 and 30 cm) and measured higher nutrient levels in the added terrestrial sediment. This is in line with observations from a study by Lovelock *et al*. (2004) involving nutrient enrichment of dwarf mangroves in Panama where 2.5 to 6 fold increase in hydraulic conductivity occurred. A separate study by Lovelock *et al*. (2006a) also noted an increase in K_L in P-fertilized dwarf *R. mangle*. Nevertheless, a hydraulic conductivity increase threshold was noted at 30 cm burial level in all the species except for *C. tagal* growing at the seaward side of the forest. It could therefore be said that at the 45 cm burial level, sedimentation stress-induced loss of conductivity outweighed the presumed nutrient-induced increase in hydraulic conductivity.

6.4.2 *Sedimentation induced changes in xylem structure*

We observed species-specific alterations in xylem structure (vessel grouping and vessel sizes) after 14 months of partial burial (Figure 6.4, Table 6.1). Such stress-induced adjustments in xylem structure have equally been reported following heavy metal contamination and imposed drought in red marple where reduction in Ks was also noted (de Silva *et al*., 2012). In the current study, both vessel grouping and diameter were found to be sensitive to sedimentation in differing magnitude and directions in the species studied.

A. marina wood which is characterised by relatively narrow vessels (Robert *et al*., 2009a), developed even narrower conduits and higher vessel grouping as a result of burial. While vessel grouping is associated with hydraulic safety (Carlquist, 1984; Carlquist *et al*., 2009; Scholtz *et al*., 2013), others have been of the view that extensive vessel connectivity increase probability of spread of embolism (Loepfe *et al*., 2007; Martínez-Vilalta *et al*., 2012). However, the argument by Lens *et al*. (2011) that grouping is compensated for by vessel diameter under water limiting conditions is thus upheld in this study. It has also been found that vessel sizes are governed by water availability, in that; limited water leads to small cambial derivatives thus formation of narrow vessels (Woodward, 2004).

In *C. tagal*, it was established that adaptation of xylem characteristics to large sedimentation events may take various forms depending on intertidal position and sediment burial level. The trees may show: (i) lower vessel grouping index (VGI) but an increase in vessel diameter (De) and potential conductive area, or (ii) higher vessel grouping with reduced De, or (iii) a reduction in both vessel grouping and potential conductive area but increasing vessel diameter. The differences in vessel characteristics (which were coupled with hydraulic conductivity variation) between the landward and seaward plots showed that local differences existing within a given intertidal area contribute significantly to within species strategies to cope with stress. Such intraspecific variation in vessel characteristics have been noted in *A. marina* and *R. mucronata* growing a long different salinity gradients with varying inundation frequencies in Gazi Bay (Robert *et al*., 2009a; Schmitz *et al.*, 2006).

In *R. mucronata*, there was a significant increase in vessel grouping in the 30 and 45 cm partially buried trees signifying a change to more xeric conditions (Carlquist, 1984). Taking into account the relatively high tolerance levels of *Rhizophora* species to hypoxia (Twilley et al. 1996), associated with sedimentation in this study, individual differences in vessel grouping index could also be could also be associated to available packing space for the vessels to occupy in the xylem (Martinez-Vilalta *et al*., 2012).

Despite all these anatomical adjustments linked to sedimentation, only vessel sizes in *C. tagal* and potential conductive area in *R. mucronata* appeared to directly explain the observed variations in hydraulic conductivity. Considering the law of Hagen-Poiseuille's, it can be said that larger vessels are quantitatively more efficient in sapflow than those with smaller diameters (Tomlinson, 1994; Choat *et al*., 2007). Additionally, high potential conductive area could provide more alternative routes for xylem sap to circumvent air-filled vessels and vessel parts (Cruiziat *et al*., 2002). A combination of high conductive area and increased vessel grouping index (VGI), which also enhances hydraulic safety (Awad *et al*., 2010; Choat *et al*., 2011) could have resulted in increased hydraulic conductivity for the 15 cm burial level in which branches had a combination of the two features (Table 6.1).

6.4.3 *Total stomatal area adjustment under sedimentation*

Despite the more negative redox potential measured in our sedimentation plots indicating increased hypoxia, we observed no significant change in stomatal area of leaves produced by *A. marina* and *R. mucronata* following partial sediment burial (Table 6.1). Dahdouh-Guebas *et al*. (2004) also found no significant differences in stomata densities in leaves in *A. marina* growing landward –less hypoxic and seaward- more hypoxic (Matthijs *et al*., 1999). The findings are however, inconsistent with those of De Deurwaerder *et al*. (2016) in the same species growing in Tudor Creek, Kenya - an area experiencing high sedimentation rates. Further, Sojka (1992) also cited an association between stomatal area and hypoxia in various plants including mangrove tree species. Nevertheless, reduced stomatal area was observed in response to partial burial in *C. tagal* (Table 6.1). Reduction in total stomata area could be interpreted as a response to lower transpiration rates against the decreased water uptake imposed by large sedimentation events in this case (Tomlinson, 1994) thus preventing critically negative xylem pressure. This is in line with findings by Lake *et al*. (2001) showing that plants can adjust their stomata development in newly formed leaves in response to prevailing conditions. This enables them to regulate transpiration thus ensuring that sap flow is maintained (Meinzer and Grantz, 1990). The interspecific variation in stomatal properties in response to sedimentation further affirms species-specific strategies in coping with stress.

6.4.4 *Resilience of mangrove tree species to large sedimentation events*

The results of this study showed adaptation mechanisms that are mostly species- and location specific and consist of: (i) improved hydraulic architecture allowing to avoid or overcome cavitation and its effects; or (ii) reduction in stomatal area which minimises transpiration for an optimal water transport capacity. Considering the relatively short period within which the anatomical changes were observed, the high plastic growth nature of plants is emphasised (Jain and Minocha, 2000). It could therefore mean that in the event of large sedimentation events, that is likely to be occasioned by flooding (Bamroongrusa and Yuanlaie 1995) as a result of torrential rains projected by the IPCC (IPCC 2007; WWF 2006), mangrove trees may adjust accordingly over short periods of time through either one or a combination of the observed adaptations to partial burial. Moreover, our results suggest that the higher hydraulic conductivity in the sedimentation treatments was in fact occasioned by the new hydraulic traits developed by the trees in response to burial. This is because the observed reduction in the soil redox potential was still within the ranges associated with higher inundation classes (Matthijs *et al*., 1999).

6.5 Conclusions and perspectives

Following 14 months of experimental partial burial simulating three levels of sedimentation event, the studied mangrove trees did not show failure of hydraulic conductivity, even in the highest burial treatment (45 cm). The results show that mangrove trees may thus acclimatise to large and sometimes episodic sedimentation events at least under the conditions that our experiment was set. Further, the results suggest a rather rapid (within 14 months) adaptation ability of mangrove trees to sedimentation-induced stress, which we relate to physiological drought in its effect on water flow. As stated in our hypothesis, vessel grouping, diameter and potential conductive area are all sensitive to sedimentation but to varying degrees among species and even individuals of the same species in the same geographic location. It is however, not always the case that the anatomical changes are reflected in hydraulic conductivity. Other than possible influence of change in vessel sizes in *C. tagal*; combination of high VGI and potential conductive area in *R. mucronata*, the results affirm that sedimentation influence sap flow positively through associated increase in nutrient input within the mangrove environment. Possibility of ion-mediated increase in K_S should however also be looked at in such future studies to ascertain the cause of the observed hydraulic conductivity patterns. This should be coupled to development of vulnerability curves to offer further insights as such increases have been associated with embolised in vessels (Hacke, 2014). It is also imperative that other fine-scale inter-vessel structures (not considered in this study) be explored to offer further explanations to the observed hydraulic conductivity patterns. Such future studies should consider longer periods of exposure, different textural classes of sediment and finer resolutions of burial levels, to determine progression of parameters measured in the current study.

.

CHAPTER 7:

Mangrove trees survive partial sediment burial by developing new roots and adapting their root, branch and stem anatomy

Manuscript ready for submission

Abstract

Background: Mangrove forests generally constitute depositional sites from a geomorphological point of view. This is facilitated by the unique root structure of the trees that may trap and retain sediment. Their roots also function as breathing structures to help mangroves cope with the hypoxic conditions of the habitat through the lenticels which are equally found on the bark.

Aims and methods: This study simulated natural and rapid sedimentation in an experiment involving partial sediment burial of mangrove trees up to 15 cm, 30 cm and 45 cm levels. The effect of the treatments on root development and bark structure of three mangrove tree species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*), common species along the Kenya coast and around the Indian Ocean, was then evaluated.

Results: There was an increase in root density over time with increased sedimentation levels which was also linked to survival following burial particularly in *C. tagal* where five of the 17 buried trees died in the 45 cm sedimentation, each of which did not form new roots. An increase in air lacuna diameter in the root cortex, and increased ray parenchyma and cylinder of secondary xylem widths was observed. There was also an induction of the phellogen, producing more outer tissue in the buried section of stems in all three studied species (2 fold increase in *A. marina* and *C. tagal* and 4 fold in *R. mucronata*).

Conclusion: The results suggest that the observed morpho-anatomical adaptations could have resulted in better performance or recovery of biological processes in the burial-affected trees. They prove that under the circumstances studied several key mangrove species stretch their adaptation to hypoxic conditions to respond dynamically and within months to sediment-burial. For these species this may signify resilience to increased terrestrial sediment input.

Contributors: Okello J.A.- main author; Robert E.M.R.- write-up, Kairo J.- experimental design, Dahdouh-Guebas F.- supervision; Beeckman H. -supervision in the lab and write-up, Koedam N.- lead promoter, experimental design and supervision

7.1 Introduction

The mangrove environment is highly variable owing to a combination of periodic fluctuations and extremes in physicochemical variables caused by the tides and coastal currents (Tomlinson, 1994). As a result, mangrove tree species have developed various adaptive mechanisms to deal with the demands of the mangrove habitat (Krauss *et al.*, 2008). Moreover, possession of these adaptive features has been attributed to the fidelity of these plants to their environment (Saenger, 2002). One of the important forms of morphological adaptation is the complex root networks for anchorage and facilitation of gaseous exchange in the hypoxic mangrove environment (Kathiresan and Bingham, 2001). This process of storage and air transport is facilitated by the presence of aerial roots and aerenchyma, a feature highly characteristic of more specialized mangroves in which some part of the root system remains exposed to the atmosphere at least at low tide (Tomlinson, 1994) with extensive coverage of lenticels (Blasco *et al.*, 1996). Mangrove roots are also characterised by a spongy cortex made up of large aerenchymal lacunae (Metcalfe and Chalk, 1957; Pi *et al.*, 2009) which enhances efficient internal oxygen transfer (Jackson and Armstrong, 1999; Colmer, 2003). Since low oxygen concentrations can impede root growth (Crawford, 1992; Drew, 1997; Armstrong and Drew, 2002), such adaptations that aid in root aeration can be critical for plant survival (Colmer and Voesenek, 2009).

Aerial roots may take five major forms which are characteristic of specific mangrove tree species or genera (Tomlinson, 1994): (i) Stilt roots are the most conspicuous forms of the aerial roots, characterised by branched loops originating from the tree trunk. This type of roots is typical of the genus *Rhizophora*; (ii) *Ceriops* and *Bruguiera* possess knee roots which form pronounced loops appearing as a blunt, knoblike structure raised from the ground; (iii) pneumatophores of *Avicennia* spp. show negative geotropism with pencil like structures protruding from the ground rarely exceeding 20 cm in height; (iv) peg roots in *Sonneratia* are similar to the pneumatophores in *Avicennia* but much stouter and may become knob or mushroom like in some cases; and (v) plank roots in *Xylocarpus* which are vertically wavy and plank-like. The aerial roots (apart from those of *Rhizophora* spp.) are attached to cable roots which run laterally below the ground.

Apart from their role in aeration and providing anchorage to the trees, mangrove roots also provide a mechanism for trapping sediment which may be introduced to coastal areas through river discharge, dumping of dredged material and floods (Wolanski, 1995; Kathiresan, 2003).

Mangrove trees create a turbulent zone maintaining the sediments in suspension letting them be deposited just before slack. The aerial roots also ensure that the deposited sediments are not re-suspended during ebb by creating an opposite force to the ebbing tides (Alongi, 2009). As a result mangroves are not just passive importers of fine particles, but structurally capture silt, clay, and organic matter (Furukawa and Wolanski, 1996; Kitheka *et al.*, 2003; Alongi, 2009). This process of sediment accumulation (accretion) is greatly influenced by size, shape, and distribution patterns of trees (Alongi, 2009) and the spatial pattern of deposition vary with distance from the seaward fringe (Furukawa and Wolanski, 1996; Kimeli, 2013).

Through accretion, mangrove trees stabilize the mud flats and create new mud banks facilitating further colonisation by this plant community (Furukawa and Wolanski, 1996; Alongi *et al.*, 2004). Long term accumulation of sediment through accretion and subsurface accumulation of refractory mangrove roots results in raising elevation hence may help mangroves adjust to sea level rise (McKee *et al.*, 2007; Smoak *et al.*, 2013). Coupled to sediment accretion, mangroves also help in filtration and retention of sediments and adsorbed nutrients from terrestrial areas (Tam and Wong, 1994) thereby protecting the offshore ecosystems (i.e. sea grass beds and corals) against siltation and eutrophication (Ewel *et al.*, 1998; Fabricius, 2005). However, with increasing demand for wood and wood products and cropland uplands, there has been rampant clearance of vegetation coverage including forests leaving the land bare and prone to soil erosion. This has increased riverine delivery of sediment from bare land and agricultural fields to the coastal areas with a potential of causing sedimentation in mangroves (Alongi *et al.*, 2004; Mohamed, 2008). Coupled with the likelihood of increased mean annual rainfall, punctuated with flash floods in East Africa (Christensen *et al.*, 2007; IPCC, 2014), the situation may worsen. Increased sediment input into the coastal areas consequently poses a major threat to mangrove forests and adjacent ecosystems (Gray, 1997).

Following the important role that mangrove root structure play in creating an enabling environment for establishment and survival of mangrove trees, and as an important agent in the process of accretion, it is crucial to determine how roots would stretch their adaptation under changed or more severe events like large sedimentation. Even though a number of studies have attempted to document below ground development of mangroves under normal accretion conditions (Young and Harvey, 1996; Purnobasuki and Suzuki, 2005; Pi *et al.*, 2009), following an oil spill (Snedaker *et al.*, 1981) and under arid conditions (Saifullah *et* *al.*, 2004), effects of increased sedimentation on mangrove below ground development are not fully understood. Ellison (1998) published cases of sediment burial of roots of different mangrove tree species, and attempted to link tree survival to root sensitivity of the different species but the large variation in response from one location to the other calls for experimental designs to explain the observations made. This study therefore evaluated the response of mangrove trees to experimental sediment burial mimicking large sedimentation event and their probable contribution to survival and/or mortality in the affected trees. The study was based on two hypotheses: 1) increased sedimentation leads to mangrove mortality through interference with the normal functioning and development of mangrove roots and the buried stem section and: 2) after sediment burial, the mangrove tree root system has to regain a similar amount of aerial roots to guarantee sufficient oxygen uptake. Specifically, the study focused on: (i) physiognomic diversification of aerial roots (ii) root anatomy and (iii) bark development, in experimentally partially buried *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata* mangrove trees in their natural setting.

7.2 Materials and methods

7.2.1 *Study site and Experimental design*

This section of the study was based on the same field experiment set up in plantations of *Ceriops tagal*, *Rhizophora mucronata*, and *Avicennia marina* at Gazi Bay Kenya (4°22′S, 39°30′E) described in chapter 5 of this dissertation. Figure 7.1a shows one of the plots in the *A. marina* stand with netting enclosure and terrestrial sediment added. A total of four plots were established for each of the species apart from *C. tagal* for which eight plots were made (four closer to the forest edge and the others more to the interior). For the purpose of this study the *C. tagal* plots at the plantation edge are termed landward (Chapter 4). The total number of trees in each of the plots and their structural attributes are given in Table S3.

7.2.2 *Field Sampling*

(a) Field surveys

Survival:

All dead branches (completely dry) were removed from all the trees within each of the plots and the total number of living branches noted at the beginning of the experiment. The trees were then assessed for signs of wilting (by observing drooping leaves) on a monthly basis and any new dry branch noted (denoted ‘branch mortality’).

Root development:

A. marina enclosures were sub-divided into four, 1 m by 1 m quadrats, using short (20 cm) pegs and assigned letters i, ii, iii and iv (Figure 7.1b). Monitoring of pneumatophore growth was only done in two diagonal quadrats (ii and iii) while standing on an adjacent one thus (and generally) avoiding trampling the pneumatophores within the sampling quadrats. Pneumatophores (where present after burial) were also counted at the beginning of the experiment and the process repeated monthly over a period of one year.

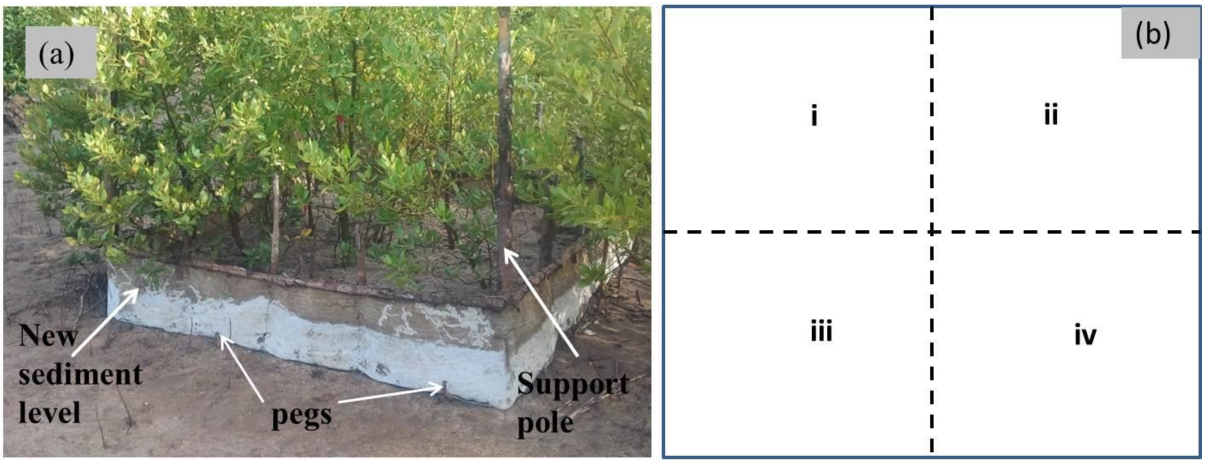


Figure 7.1 **(a)** One of the experimental sedimentation *A. marina* plots in the study site **(b)** a diagrammatic bird’s eye view representation of *A. marina* experimental plots. The dotted lines are the short pegs which were used to subdivide the plot into four quadrats.

All aerial roots of *C. tagal* were buried by sediment at the beginning of the experiment. Subsequent sampling was done when the first aerial roots were observed above the sediment (after 20 months). Assessment of development was based on ease of visibility of the knee roots appearing above the new sediment level and reported as (i) not visible: - no roots seen, (ii) slightly visible: - just appearing from the tree trunk and only seen through slight removal of some sediment, and (iii) visible: - seen clearly protruding above the sediment.

Stilt roots in *R. mucronata* that remained exposed after partial burial at the onset of the experiment were counted per tree and grouped as hanging and fixed at that time (hanging roots usually becoming fixed subsequently). New roots and dead ones were assessed and grouped accordingly during the subsequent monthly sampling. These were done in all the trees within the plots.

After two years of partial sediment burial, two living trees, one from the 45 cm and the other from controls of each of the three studied species were excavated. A slit was made on the side of the net close to the tree to be excavated in the silted plots using a pair of scissors. Sediment was then carefully removed around the tree using sharp pegs while ensuring that the root structures are maintained. Some seawater was then splashed on the exposed roots to release the mud in order to have a clearer view of the root features. Structural development of the aerial roots was then observed in the sections that were once exposed to the atmosphere and buried after the treatment and any anomaly with respect to controls recorded. The sediment was also dug deeper to access the original cable roots that were present before sedimentation using a hoe (Plate 7.1).

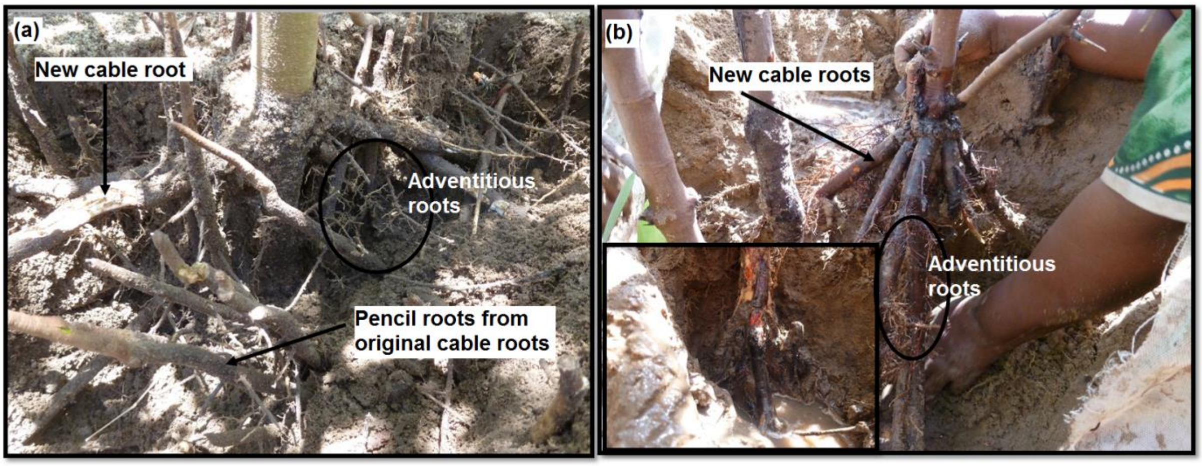


Plate 7.1 Mangrove trees dug out in one of the sedimentation experiment plots to expose new/ original roots **(a)** in *Avicennia marina* **(b)** in inset original *Ceriops tagal* roots below, after 2 years of partial burial

(b) Roots and stem sampling for anatomical analysis

Small pieces (5 – 8 cm) of the different root types for both the original (present before sedimentation) and new (developed after burial) were then sampled from the partially buried trees. Cable roots (in *A. marina* and *C. tagal*) and stilt roots (in *R. mucronata*) were cut from two points, 5 cm away from trunk and mid distance from root tip to the trunk (Figure 7.2a). Two to three samples of the different root types were collected from the aforementioned sections giving a total of 21. Pneumatophores in *A. marina* were sampled from both new cable roots and original cables as well as above and below sediment level. Two to three samples in each case were collected giving a total of 32. These were cut 4 cm from the tip of the exposed section and 4 cm below sediment level. Similar samples were also collected from the controls for comparison. The samples were cleaned with water and stored in a mixture of 70% ethanol (CH_3CH_2OH) with a few drops of glycerol ($C_3H_8O_3$) for anatomical analysis.

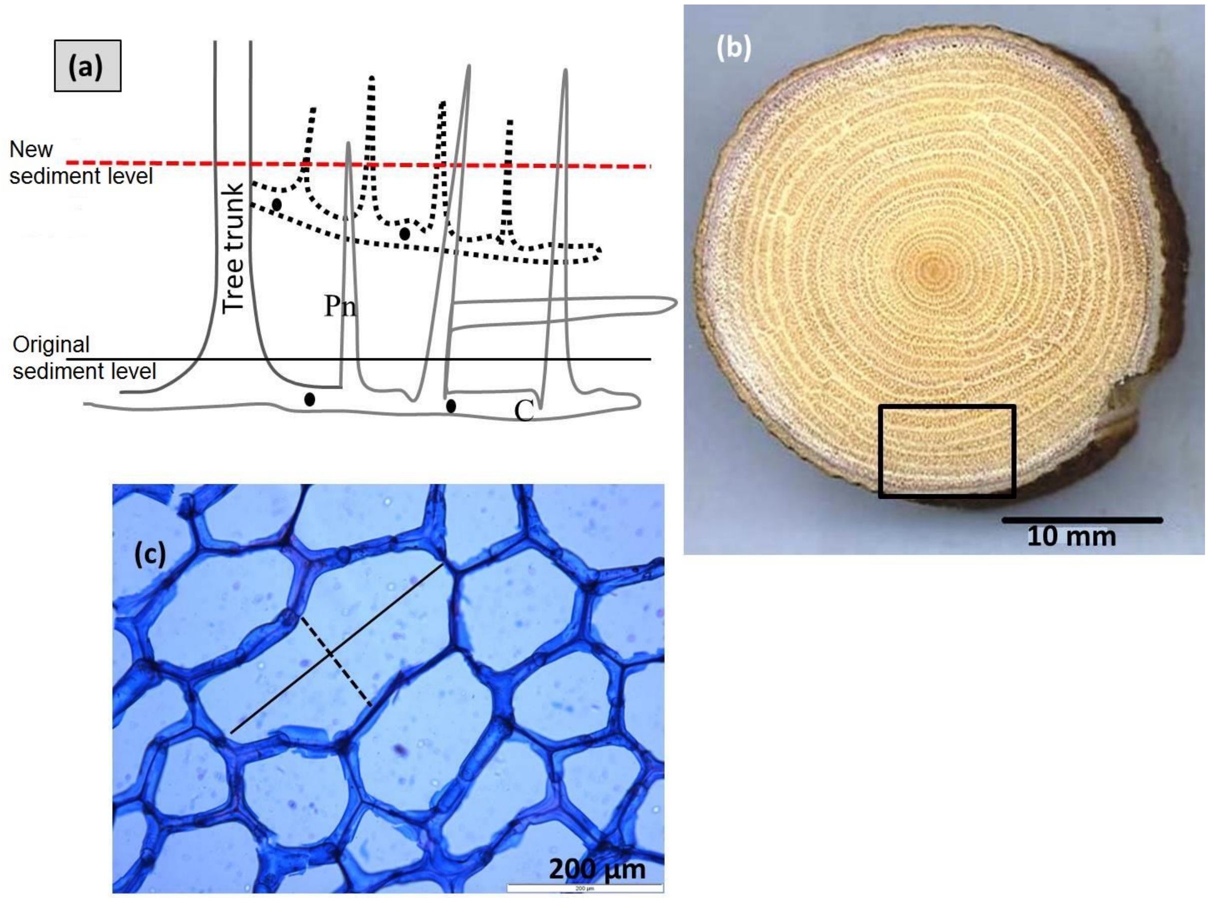


Figure 7.2 (a) A diagrammatic representation of the pneumatophores in *A. marina* after 2 years of partial sediment burial (C = cable root, Pn = pneumatophores from the original roots while the dotted lines are the new roots). Sampling of different root parts was done at the points indicated by black dots. **(b)** Piece of stem disc of *A. marina* showing the position of sawing for sectioning **(c)** cortex in one of *A. marina* pneumatophore sampled below sediment. Continuous line and dotted lines are the first and second measurements of an air lacuna respectively.

The trunk below the new sediment level was also assessed for any observable changes between the periods before and after burial. All the trees from which root samples were collected (including the controls) were then cut down and an 8 cm piece of the main stem cut 5 cm below and above the sedimentation level (Figure 7.2a). Three 0.5 cm^3 pieces were then cut as shown in figure 7.2b and immediately stored in alcohol – glycerol mixture. The remaining piece of about 3 – 5 cm long was cut and air dried.

7.2.3 *Root and bark anatomy*

(a) Sample preparation

The alcohol – glycerol preserved root samples were cut in to 8 – 10 mm long segments. In the case of large stilt/ cable roots, the samples were further cut radially from the centre for ease of handling. These were then soaked in polyethylene glycol (PEG) with molecular weight 1500 (Pure, VWR International, Prolabo) in the oven at 60 ºC for 24 hours. The soaked samples were then embedded with fresh PEG 1500 for another 24 hours at room temperature to enhance the cells' integrity and avoid tearing of sample during sectioning (Wolosewick, 1980). Transverse sections of 25 – 30 µm thickness were made from the PEG embedded samples using a microtome (Lab-Microtome, Holger Gätner) and stained using safranin-alcian blue mixture. The staining solution for which was prepared by dissolving 0.35 g safranin in 35 ml 50% alcohol, mixed with 0.65 g alcian blue dissolved in 65 ml distilled water. Sections were then mounted on glass slides using Canada balsam (Merck). The 0.5 cm^3 alcohol – glycerol mixture preserved stem cubes were also impregnated with PEG to prevent the bark from peeling away during sectioning. Sectioning, staining and mounting were done following similar steps described above for the roots.

The air dried pieces of stem were sanded using a series of sandpaper from 50 to 1200 grit to smoothen the transverse sections to improve visibility of the tissues. The wood samples were then further cut using a hand saw into disks of about 1.5 cm thickness.

(b) Anatomical observations and measurements

Macroscopic observations of the stem discs were made under a stereo microscope (Olympus SZ) and measurements of the cork tissue done using ImageJ 1.45s, (Wayne Rasband, National Institute of Health, USA). The micro-sections of the bark were viewed under a microscope (Olympus BX60) fitted with a camera (Olympus UC30) and any anatomical variations between the discs cut below and above sediment noted. The root sections were also viewed under microscope and measurements done using basic image-acquisition and archiving software CellB (Olympus Cell^B Soft Imaging System GmbH, Münster, Germany). Air lacunae 'diameter' was obtained by averaging the longest distance across the aperture of the intercellular spaces and the mid perpendicular length across the first measurement (Figure 7.2c). Additionally, the cylinder of secondary xylem[▲] and cortex widths was measured from which a ratio was obtained to determine the size of the cylinder in relation to the air spaces

---

[▲] Cylinder of the secondary xylem is part of transport system of vascular plants whose main components are xylem and phloem tissue with the cambium normally occurring between the two tissues.

($\frac{Cortex\ width}{Width\ of\ cylinder\ of\ the\ 2^0\ xylem}$). In *R. mucronata* roots, the widths of ray parenchyma were measured at four random points along each set of rays under four different microscopic fields of view. All the microscopic measurements were done in four fields of views of about 0.385 mm^2 (objective x 10) or 2.387 mm^2 (objective x 4).

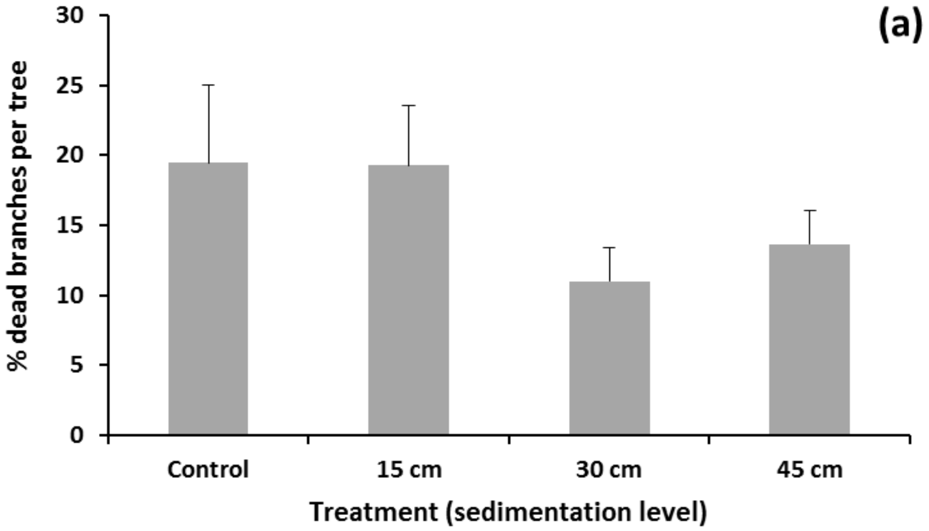
7.2.3 *Analysis*

Data analysis was done in Excel (Microsoft office 2010) and STATISTICA 7.0 (StatSoft Inc., Tulsa, USA). Data sets were tested for normality and homogeneity of variances and where conditions were met, a parametric test (One way ANOVA) was used to test for differences across treatments otherwise a non-parametric test (Kruskal-Wallis ANOVA by ranks) was applied. Mann-Whitney U test was used to test for differences between bark thicknesses of stem below and above sediment. The test was also used in determining the difference in ray parenchyma thickness between new roots in silted and controls of *R. mucronata*. Spearman rank correlation was then used to determine relationship between root visibility and branch mortality in *C. tagal*. Since the difference between cortex-cylinder of secondary xylem ratio of cable roots from sections close to trunk (5cm) and away from trunk was not significant, the two sets of data were pooled in subsequent analysis.

7.3 Results

7.3.1 *Mortality*

Branch mortality with respect to partial burial varied from one species to the other. There was reduced branch mortality in *A. marina* with the trees under burial (30 and 45 cm) having lower branch mortality than the controls (Figure 7.3a). The highest percentage reduction (8.5%) in branch mortality relative to the controls was observed in the 30 cm silted trees. In *C. tagal* branch mortality increased with increase in sedimentation level in both the seaward plots and the landward plots. There was however no significant difference between the landward and seaward plots despite the visual differences indicating relatively higher branch mortality in the former than latter (Figure 7.3b). A multiple comparison of means revealed that it was only the 45 cm partially buried trees that had significantly higher branch mortality than the controls and all the other sedimentation levels ($F=12.13$, $p<0.001$).



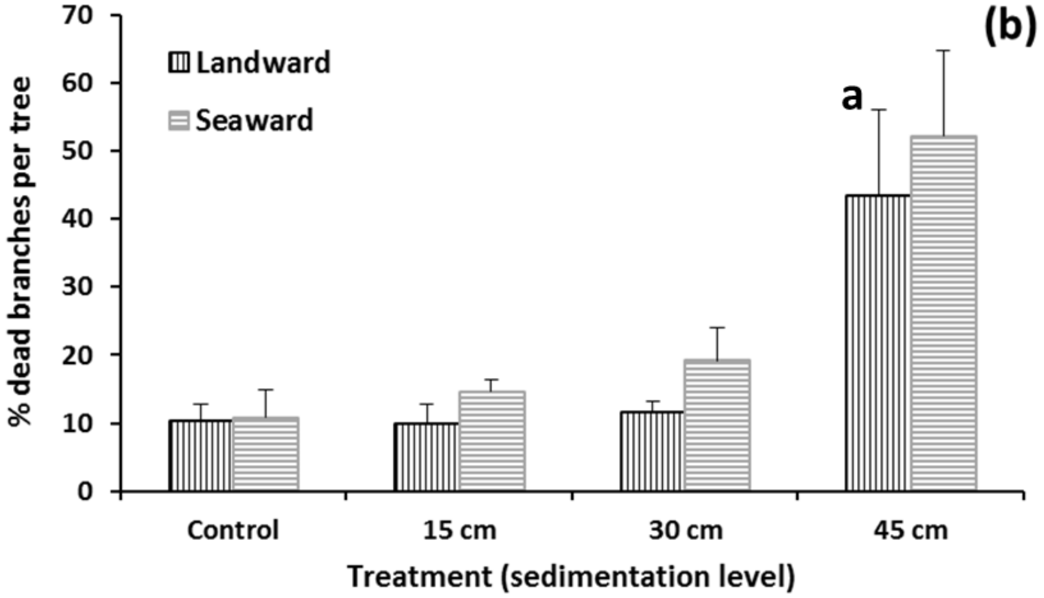


Figure 7.3 Branch mortality in mangrove trees **(a)** *Avicennia* and **(b)** *Ceriops*, under partial sediment burial of different levels. The marked bars in b are significantly different from the others.

Ceriops was the only species of the three studied species where total tree mortality was experienced and was only observed in the 45 cm sedimentation level. In the seaward plot, two out of the eight buried trees died while three out of the ten died in the landward plot. The first death was observed in the landward plot three months into the experiment while the first seaward tree died after five months. It was also noted that all the *C. tagal* trees that died had not developed new roots but instead their stem rotted away (Plate 7.2c). Moreover a highly significant negative correlation was established between root visibility in this species and percentage branch mortality (rs= -0.58, p < 0.001). In *R. mucronata*, exceptionally high branch mortality was only observed in the 45 cm silted plot and in only one of the silted trees (36.8% of the total branch count). The rest of the trees in all the treatments had very low branch mortality ranging between 0 and 3.0% of the total branch count.

7.3.2 *Root physiognomy*

Whereas the trees in the controls maintained more or less the same number of aerial roots over the experimental period, the partially buried trees produced new roots which could be observed above the new sediment level after different period of time depending on the sedimentation level and the species (Plate 7.2a, b and d; Figure 7.4).

Plate 7.2 New aerial roots (black continuous arrows) appearing above the new sediment level in 45 cm partially buried **(a)** *A. marina* **(b)** *C. tagal* **(d)** *R. mucronata*. Trees that did not produce aerial roots in *C. tagal* **(c)** dried out. Dotted arrows in **(d)** are original prop roots.

A. marina formed new cable roots that emerged from the stem about 2 – 5 cm below the new sediment level (Figure 7.2a). From this cable root, pneumatophores developed which could be seen from above the sediment while the pneumatophores from the original cable root also grew longer to reach the new sediment surface (Plate 7.2a). Branching of pneumatophore was more frequent in the partially buried trees as compared to the control. This branching was observed in the pneumatophores from the original cable root which also became fluffy in nature and developed numerous adventitious roots. *C. tagal* formed new knee roots which could be observed close to the trunk above the sediment (Plate 7.2b). New cable roots also developed about 2 cm below the new sediment level and these too had several adventitious roots. The cable roots however appeared to be positively geotropic (growing downward) unlike the original cable roots and those in the control which lay parallel to the ground level. *Rhizophora* formed new stilt roots above the new sediment level (Plate 7.2d) at higher rates than control trees. Below the new sediment level were also new roots with numerous adventitious roots while the original stilt roots produced hypertrophied lenticels on the portion that was covered below the sediment. The originally exposed stilt roots also developed root branches which were equally covered with adventitious roots below the sediment.

The first new aerial roots appearing above the sediment in the highest sedimentation level in *A. marina* were observed after four months of burial (Figure 7.4a) while in *R. mucronata* trees, the first new hanging roots were observed after 5 months (Figure 7.4b). Once the first new roots were observed in the partially buried trees, there was a further increase in densities with time, the peaks levelling out after 11 months in *A. marina* and 6 – 7 months in *R. mucronata* (Figure 7.4a and b). The rate of development of the new aerial roots was also higher with increase in level of partial burial in both *A. marina* and *R. mucronata*. New roots in *C. tagal* were first seen in the 45 cm seaward plot after nine months of burial while the others appeared much later in the experiment (Table 7.1). After 20 months into the experimental period, the visibility above sediment of the new roots in the trees was as shown in figure 7.4c and d.

Table 7.1 First incidence of observation of knee roots above sediment in partially buried *Ceriops tagal* trees

Treatment (sedimentation level)	**Period after burial**	
	Landward	**Seaward**
Control	Roots not buried	Roots not buried
15 cm	11 months	10 months
30 cm	10 months	11 months
45 cm	12 months	9 months

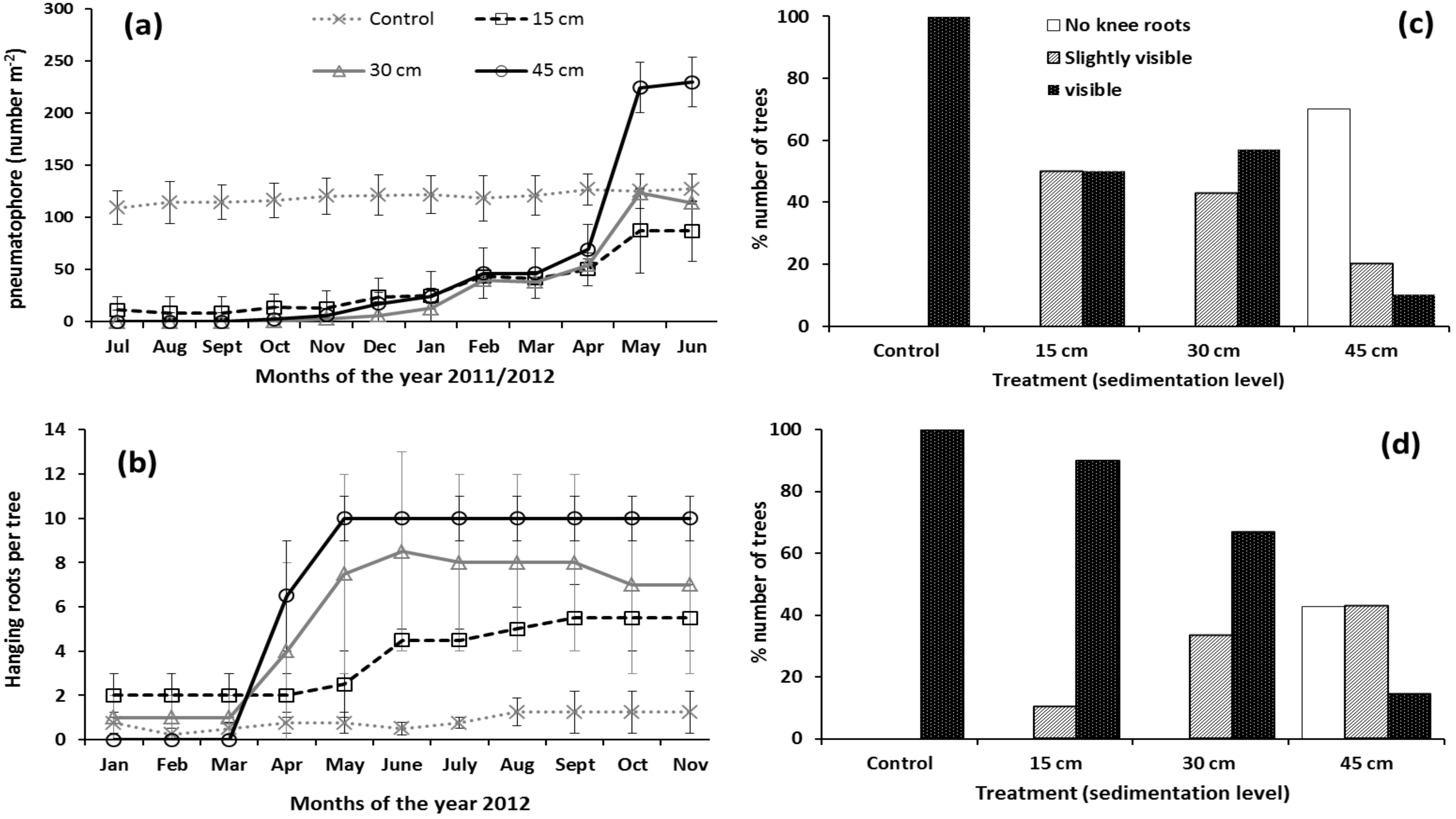


Figure 7.4 **(a, b)** Mean ± SE ; **(a)** Pneumatophore density per m^2 in partially buried *A. marina* trees, **(b)** hanging stilt roots per tree in partially buried *R. mucronata* during one year of burial; **(c, d)** Root visibility in *C. tagal* after 20 months of exposure to sedimentation in **(c)** landward and **(d)** seaward plots. (Numbers of trees per plot are as in Table S3).

7.3.3 *Root anatomical structure*

In all the three studied species the original roots in the partially buried trees remained alive despite the formation of new ones. Plate 7.3, 6.4 and Table 7.3 gives a pictorial summary of the anatomical changes observed in the roots of the different studied species. The basic anatomical features of the new roots formed as a result of the increased sedimentation were similar to their respective originals and controls (Plates 6.3 and 6.4). However, certain variations were observed with respect to specific features. In *A. marina* the difference in lacuna diameter among pneumatophores from control, original and new ones was highly significant (H= 67.62, p<0.001).

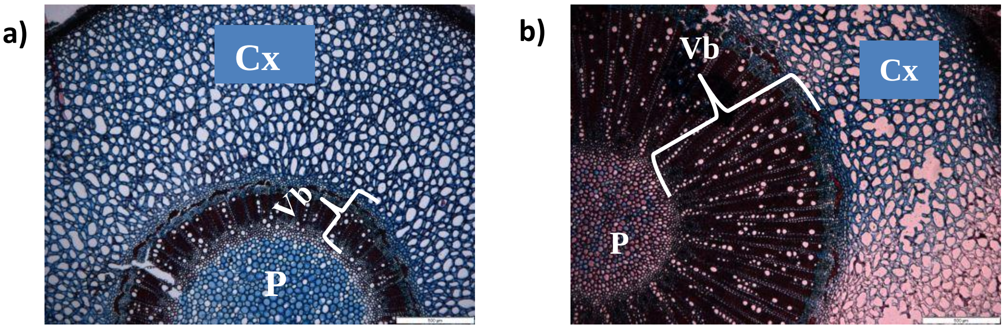


Plate 7.3 Section of *Avicennia marina* pneumatophores (scale bar = 500 µm) **(a)** from the controls above sediment **(b)** from the original root in the buried treatment above the new sediment level. **P**= pith, **Vb**= cylinder of secondary xylem, **Cx**= cortex.

The pneumatophores from the original cable roots and the new ones were found to possess cortex with larger air spaces than those of the controls. The piths had relatively larger intercellular air spaces in the pneumatophore sections buried below sediment (Table 7.2). The cylinder of secondary xylem region was relatively larger in both new and original pneumatophores above the sediment in the partially buried trees as compared to the controls (Plate 7.3; Tables 7.2). The difference among these of which was highly significant (H=29.03, p<0.001).

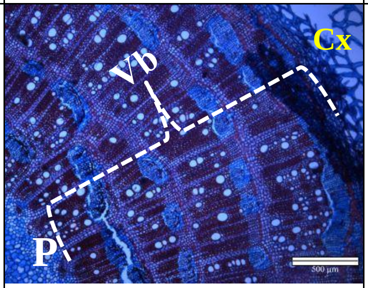
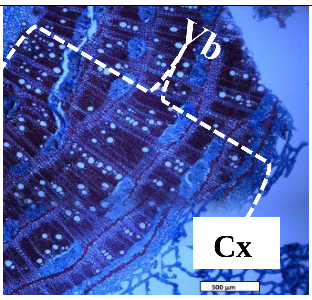
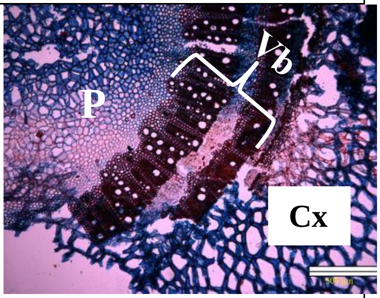
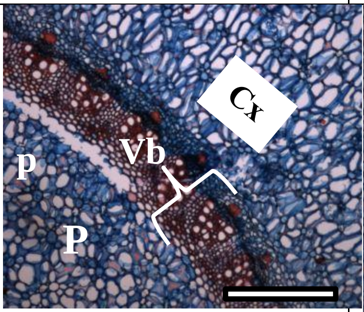
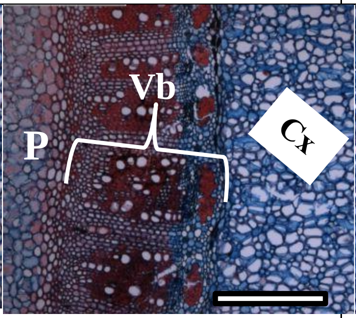
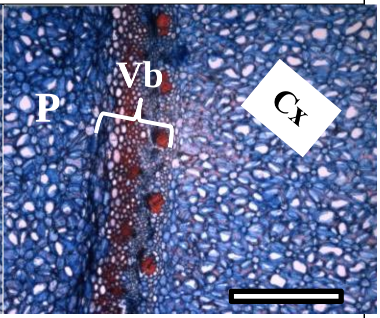
Table 7.2 Mean (±SE) diameter of the air lacunae and cortex-cylinder of secondary xylem ratio in the pneumatophores of silted *A. marina* trees after two years of exposure to partial burial

Pneumatophores		Air lacunae diameter* (µm) cortex	pith	Mean cortex/ vascular bundle ratio
New ●	below sediment	70.03 ± 2.40	35.94 ± 1.32	4.60 ± 0.07
	above sediment	57.93 ± 3.63	absent	1.07 ± 0.02
Original Ø	below sediment	133.25 ± 8.44	61.52 ± 2.43	3.14 ± 0.23
	above sediment	55.14 ± 1.73	absent	1.02 ± 0.03
Control	below sediment	62.83 ± 1.62	27.78 ± 4.83	3.76 ± 0.16
	above sediment	48.92 ± 2.24	absent	3.42 ± 0.10

● Pneumatophores emerging from cable roots formed after partial burial; Ø pneumatophores from the original cable root in partially buried trees; *obtained from mean of shortest and longest aperture length

The cable roots in *A. marina* were similar in the silted trees and the controls and no observable changes were seen in the original cable root. The cylinder of secondary xylem had internal phloem (typical of this species; Robert *et al.*, 2011) in the xylem tissue with the new roots beginning to develop similar features (Table 7.3). In silted *C. tagal* trees, the original cable root invested more in formation of a larger cylinder of secondary xylem as compared to the cortex while the new cable roots were formed with relatively larger cortex (Table 7.3). The cortex /cylinder of secondary xylem ratio for the controls was significantly different from the original but not from the new roots (H=28.95, p<0.001 and >0.05 respectively).

Table 7.3 Images of the cable roots of the *A. marina* and *C. tagal* (scale bar = 500 µm). Values in parenthesis are mean (±SE) Cortex-cylinder of secondary xylem ratio. **P**= pith, **Vb**= cylinder of secondary xylem, **Cx**= cortex

Species	Control	Original	New root
A. marina	 (1.59 ± 0.04) µm	 (1.52 ± 0.26) µm	 (4.45 ± 0.16) µm
C. tagal	 (14.95 ± 0.31) µm	 (8.19 ± 0.21) µm	 (28.10 ± 0.56) µm

In *R. mucronata*, a difference between the newly developed prop roots and the controls was observed in the xylem region and the pith. New roots formed below sediment had smaller sized air lacunae in the pith and cortex than in the controls (Plate 7.4). The new roots also had narrower bands of ray parenchyma as compared to those of the controls (U= 106, p<0.001; Plate 7.4). The mean diameter of the ray parenchyma in the two roots were 176 ± 16.52 µm while that in the newly formed prop roots of buried trees was 81.55 ± 5.95 µm. *Rhizophora*'s new roots formed below sediment had smaller sized air lacunae in the pith and cortex than in the controls (Table 7.2).

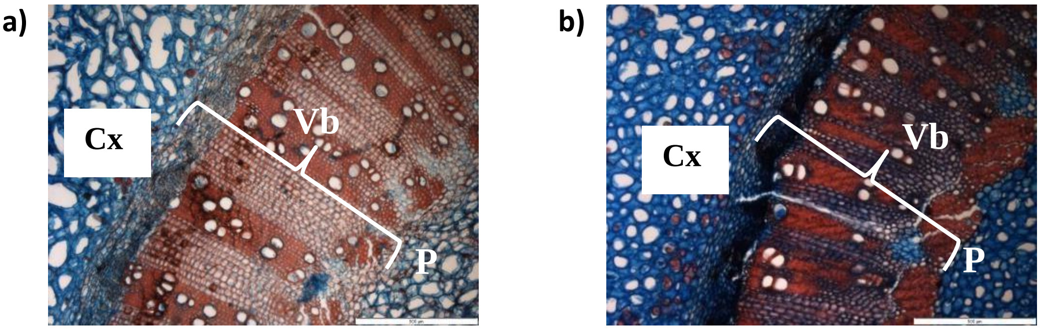
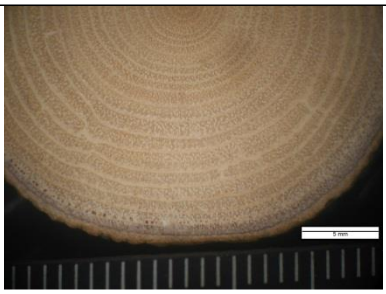
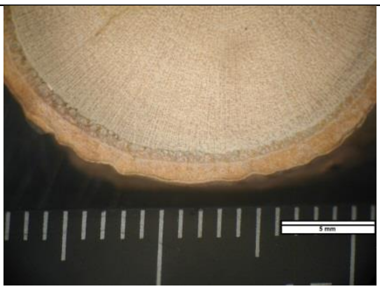
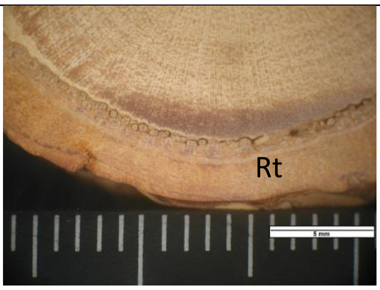
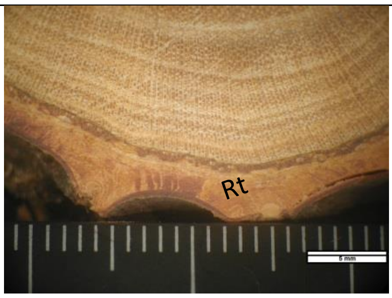
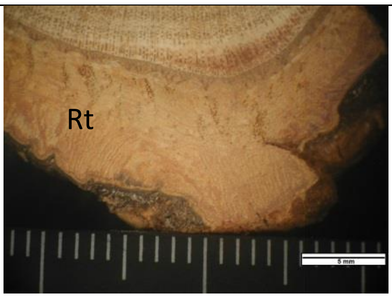


Plate 7.4 Section of *R. mucronata* stilt roots (scale bar = 500 µm). **(a)** below sediment in the control **(b)** newly formed below sediment in the buried trees. **P** = pith, **Vb** = cylinder of the secondary xylem, **Cx** = cortex

7.3.4 The anatomical structure of the bark

The partially buried trees in all the three species developed a substantial amount of bark tissue on the stems below the new sediment level (Table 7.4).

Table 7.4 Development of bark in partially buried trees of the three studied species indicating the rhytidome (Rt), (scale bar = 5 mm). Values below are mean ±SE bark tissue thickness

Species	**Transverse section of stem**	
	Above sediment	**Below sediment**
A. marina		
	574.1 ± 29.79 µm	2045.38 ± 21.68 µm
C. tagal		
	1023.82 ± 57.84 µm	2979.64 ± 103.25 µm
R. mucronata		
	2630.92 ± 136.47 µm	5665.09 ± 449.94 µm

The difference between bark thickness of stem below and above new sediment level was highly significant in all the three studied species ($p<0.001$) while this was not the case for the stems from control trees ($p>0.05$). The periderm layers on stem portions below the new sediment level were about 2 fold thicker in *A. marina* and *C. tagal* and 4 fold in *R. mucronata* (Table 7.4).

While the buried stems developed both an extended phellem (cork) and phelloderm with more spongy areas in the buried stems of all the species resulting in the increased bark thickness, the buried section of the original stilt roots of *R. mucronata* developed more layers of periderm resulting in formation of a rhytidome (Plate 7.5). In addition, *A. marina* and *R. mucronata* formed hypertrophied lenticels on the bark below sediment while *C. tagal* developed thick powdery substance that covered the bark. The powdery substance which has not been identified yet in the current study was however not present on stems of trees in the control even below the sediment.

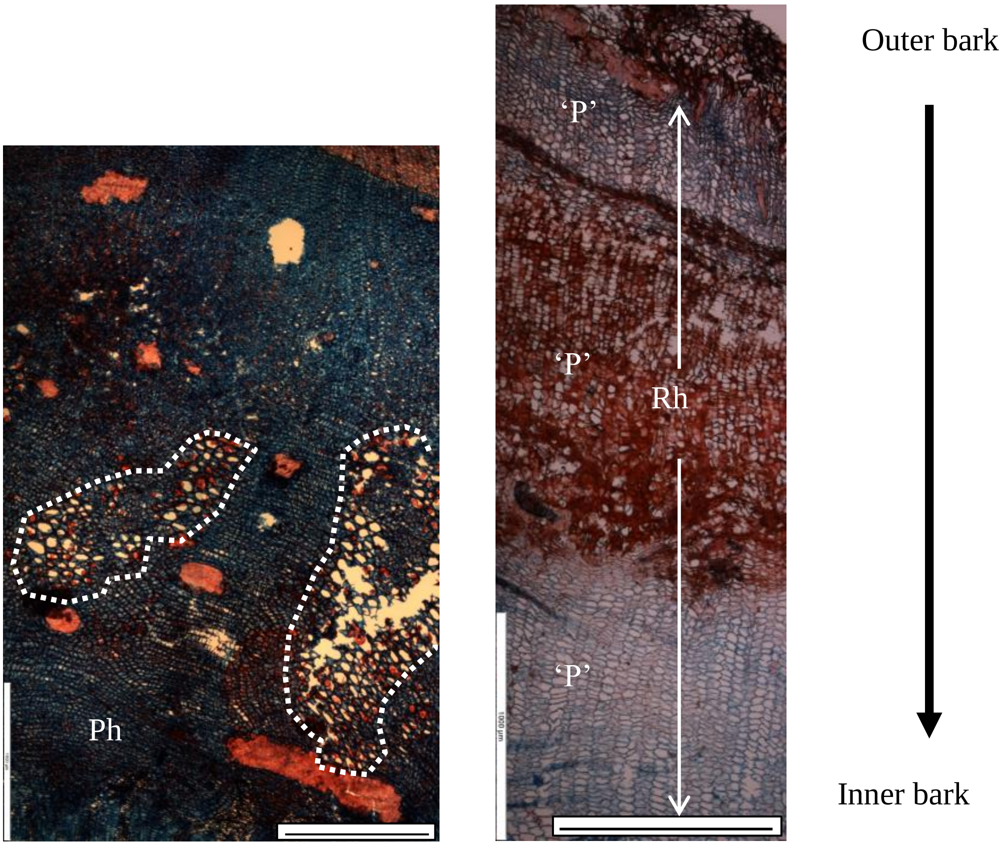


Plate 7.5 (a) Bark of *R. mucronata* stilt root above sediment showing the cork aerenchyma (encircled with the dotted lines) and the phloem marked P_h. **(b)** Layers of additional periderm marked 'P' forming rhytidome (R_h) in barks of stilt roots after burial with sediment (scale bar = 1000 µm).

7.4 Discussion

The results of this study show that sedimentation triggers a series of morphological and anatomical reactions in roots and barks of buried mangrove trees probably aimed at aiding them cope with the change through stretching their adaptation hence facilitating resilience.

Sedimentation has been noted to result in modifications of bark tissue structure in different ways which are more or less similar to observations made under prolonged flooding conditions (Yáñez-Espinosa and Flores, 2011). The increase in thickness of stems buried below sediment as a reaction to burial in this experiment is also similar to observations made in mangrove seedlings exposed to prolonged flooding (Xiao *et al.*, 2010) and in submerged portions of *Fraxinus* stems (Voesenek *et al.*, 2004). In a study by Junghans *et al*. (2004), increase in parenchyma was attributed to the influence of the phytohormone, ethylene, which is associated with cambium activity and the production of which was found to increase under flooding conditions where it stimulated growth of bark (Savidge, 1988). Ethylene has also been found to result in development of adventitious roots and aerenchyma in flooded maize, similar to observations made in the current study. Increase in cork tissue improves the trees' capacity to tolerate partial burial as more cork aerenchyma are formed creating more intercellular spaces for oxygen transport and storage (Lambers *et al.*, 1998; Wong, 2004). The resultant production of additional cork could provide an increased protective layer restricting entrance of pathogens which may come from the sediment now covering the stem (Beck, 2010). The development of hypertrophied lenticels in the portion of *A. marina* stem buried below sediment has also been observed in stem portions *A. germinans* and *Rhizophora mangle* stilt roots immersed under water over prolonged periods of time (Yáñez-Espinosa and Flores, 2011). These features were also found to be present in a number of mangrove associates stems when exposed to flooding (Mielke *et al.*, 2005).

Production of more aerial roots in *A. marina* and *R. mucronata* with increase in sedimentation level confirms the proposal by Young and Harvey (1996) that increased aerial root density ensures maintenance of balance between the benefits of aeration and the drawbacks of sediment accretion. In the current study however, the pneumatophore density increase in *A. marina* was not only from the original cable root but also through development of new cable roots a feature which has never been reported before. The observation of positively geotropic roots observed in this study is also unique as cable roots are generally expected to spread horizontally in the soil (Yáñez-Espinosa and Flores, 2011). Increased cumulative rate of growth and branching nature of pneumatophore observed in the partially buried trees have earlier been reported in two separate studies. The pneumatophores of mangroves of the Arabian Gulf began to branch after an oil spill (Böer, 1993) while increased pneumatophore elongation was reported by Saifullah and Elahi (1992) in oil polluted mangroves of Karachi.

The production of numerous adventitious roots from new prop roots below sediment in *R. mucronata*, buried portions of pneumatophores in *A. marina* and cable roots in *C. tagal* have also been observed in flooded trees. Adventitious roots in pneumatophores were observed in mangroves of the Arabian Gulf after the 1991 Gulf war (Böer, 1993) and in roots of flooded maize. Formation of larger air lacunae in the cortex and pith of the buried pneumatophores could also be attributed to need for efficient air supply even with burial. Similar observations have been made in trees without cork aerenchyma in their barks which developed larger air spaces in the phloem parenchyma and primary cortex with flooding (Roth, 1981 cited in Yáñez-Espinosa and Flores, 2011). The increased xylem ratio in the exposed section of pneumatophore in silted trees could be as a means of compensation for strength as the lower section became fluffy due to increased intercellular air spaces. The development of aerenchyma during prolonged flooding and formation of adventitious roots have also been linked to production of the phytohormone ethylene (Drew *et al.*, 1979; Jackson *et al.*, 1985; Visser *et al.*, 1996). Since oil pollution results in hypoxic conditions by slowing down rates of oxygen diffusion (Sang-Hwan *et al.*, 2007), while flooding also displaces air from the sediment (Armstrong and Drew, 2002), the similarity in morpho-anatomical response among oil polluted, flooded and partially buried mangrove trees suggests a possible increase in hypoxia associated with sedimentation.

The general changes in root system architecture and anatomy observed with burial affirms their highly plastic development hence adaptability to new environmental conditions which is associated to the continual propagation of new meristems in the root cap (Williamson *et al.*, 2001). Moreover, the root cap has been suggested to be able to sense stimuli from its immediate surrounding hence trigger a series of reactions that direct growth towards or away from unfavourable environmental cues (Kumpf and Nowack, 2015). The result is a morpho-anatomical adaptation such as those observed in this study for instance to enhance oxygen storage and transport (larger air lacunae). Consequently such adaptations may also mean an even better performance of biological processes and as such the trees may grow as though partial burial did not signify stress. This could explain the reduced branch mortality observed in *A. marina* with increased sedimentation levels. Such adaptations were observed to improve water absorption by roots in prolonged flooded trees leading to increased photosynthetic rates in a seasonal wetland in Venezuela (Herrera, 2013). Similarly, with the anatomical and morphological adjustments in the study, the trees did not show inhibitory responses due to sedimentation. However, since *C. tagal* produced roots much later into the sedimentation period this must have probably led to the higher mortalities recorded in the highly silted trees. Moreover, the fact that branch mortalities in controls of both landward and seaward plots were similar is a clear indication that the observed variations in treated plots were as a result of partial burial; and that in this species, sedimentation reached the inhibitory level leading to mortality in the highest treatment plots. In *R. mucronata*, the trees showed low branch mortalities which could be attributed to natural tree death with development. The high branch mortality observed in one of the highest partially buried trees (45 cm) signifies limited tolerance as a result of less root development by the particular tree.

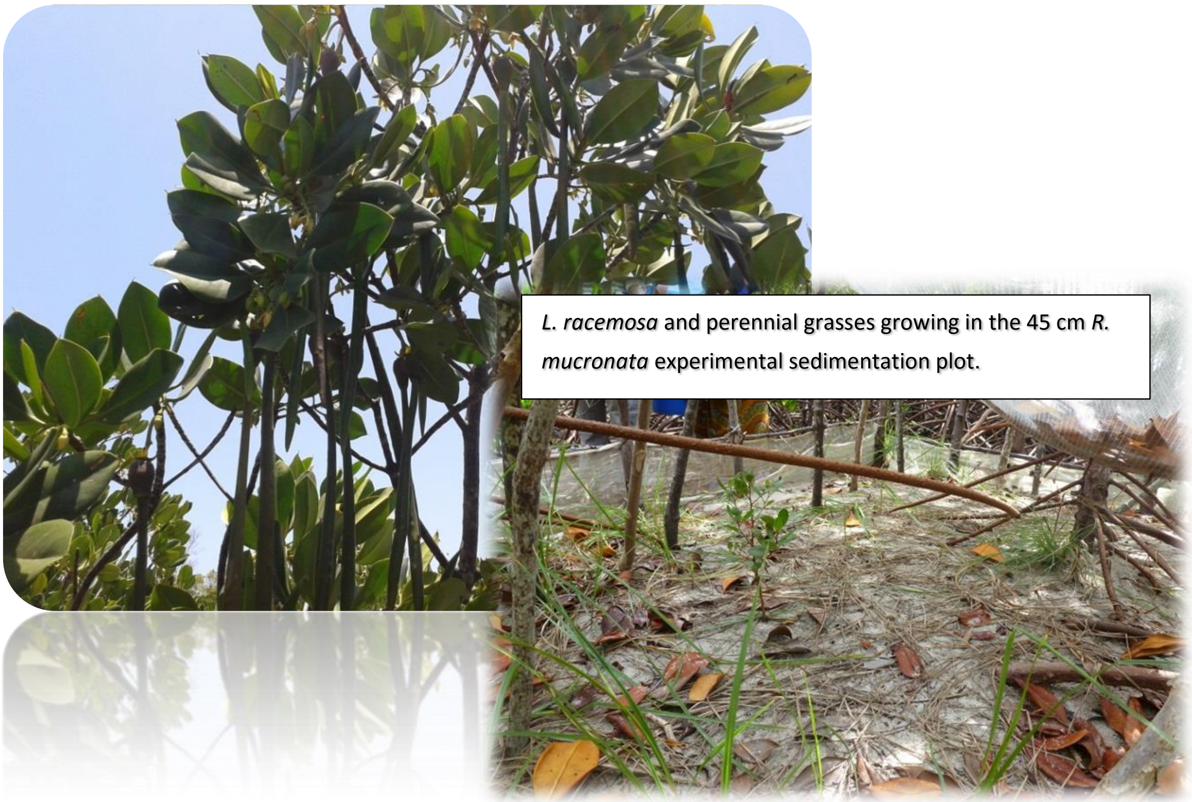
7.5 Conclusion

Sediment burial produced a more or less similar reaction on the three studied mangrove species as does prolonged flooding. As a result, the mechanism that leads to death of mangroves during sedimentation could be similar to that of flooding. Though tree mortality occurred (only in *Ceriops tagal*), we have not reached the threshold of full mangrove loss with the sedimentation conditions we imposed. This is remarkable because the trees underwent 8-33% burial of their initial height. The plasticity of roots and bark on exposure to induced sedimentation observed in this study could therefore be an important trait in ensuring survival of the trees following spontaneous large increase in sediment levels as long as the causative agent is not continuous. Moreover, inhibitory responses were not observed in *A. marina* and *R. mucronata* and only at sedimentation levels higher than 15 cm in *C. tagal*. The fact that each species responded at different paces suggests that increased levels of sedimentation would affect their distribution according to their threshold tolerance levels with the more sensitive species succumbing faster.

PART IV

Synthesis:

General discussion - Conclusions and perspectives

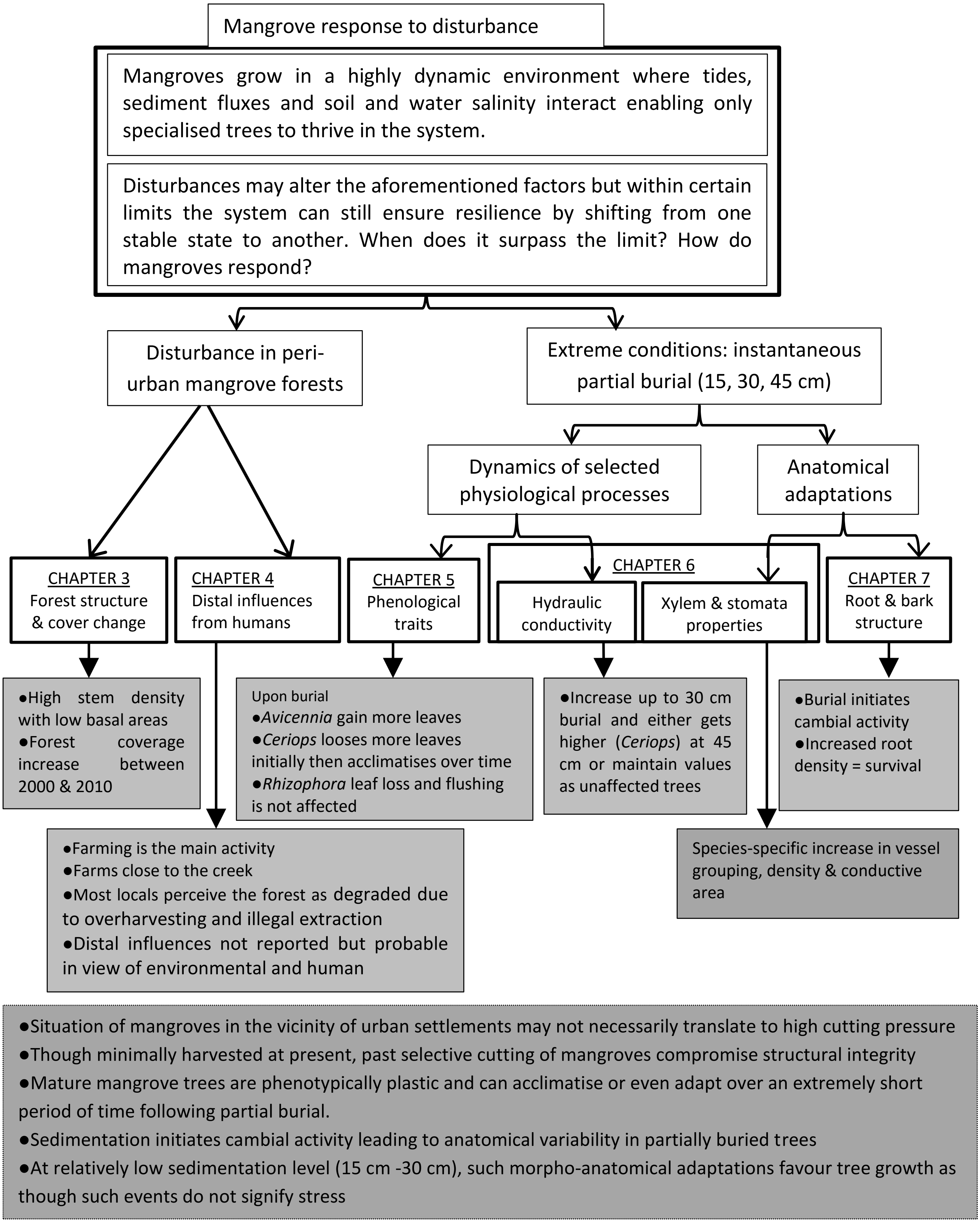


L. racemosa and perennial grasses growing in the 45 cm *R. mucronata* experimental sedimentation plot.

“I can see no other greater nor finer technology than man fulfilling the laws of nature.” **Yanosuke Nakano (1968), The right path to industrial development.**

CHAPTER 8: General discussion - Conclusions and perspectives

8.1 Summary of the findings



Mangroves grow in a highly dynamic environment where tides, sediment fluxes and soil and water salinity interact enabling only specialised trees to thrive in the system.

Disturbances may alter the aforementioned factors but within certain limits the system can still ensure resilience by shifting from one stable state to another. When does it surpass the limit? How do mangroves respond?

- ●High stem density with low basal areas
- ●Forest coverage increase between 2000 & 2010

Upon burial
- ●*Avicennia* gain more leaves
- ●*Ceriops* looses more leaves initially then acclimatises over time
- ●*Rhizophora* leaf loss and flushing is not affected

- ●Increase up to 30 cm burial and either gets higher (*Ceriops*) at 45 cm or maintain values as unaffected trees

- ●Burial initiates cambial activity
- ●Increased root density = survival

- ●Farming is the main activity
- ●Farms close to the creek
- ●Most locals perceive the forest as degraded due to overharvesting and illegal extraction
- ●Distal influences not reported but probable in view of environmental and human

Species-specific increase in vessel grouping, density & conductive area

- ●Situation of mangroves in the vicinity of urban settlements may not necessarily translate to high cutting pressure
- ●Though minimally harvested at present, past selective cutting of mangroves compromise structural integrity
- ●Mature mangrove trees are phenotypically plastic and can acclimatise or even adapt over an extremely short period of time following partial burial.
- ●Sedimentation initiates cambial activity leading to anatomical variability in partially buried trees
- ●At relatively low sedimentation level (15 cm -30 cm), such morpho-anatomical adaptations favour tree growth as though such events do not signify stress

Figure 8.1 A diagrammatic summary of the findings from the thesis; bolded box comprises the aspects studied; grey boxes with margin are specific results while the bottom grey box contains the general findings encompassing the specific areas covered. The arrows with closed arrow heads point to the main findings of each aspect studied

8.2 Disturbance influences forest structure

Mangroves have successfully adapted to the conditions in their highly dynamic environment (Saenger 1982; Tomlinson 1994; Kathiresan and Bingham 2001) which would otherwise not favour other trees and shrubs. Notwithstanding the potential threat of overexploitation on this resource to cater for the rising demand of its wood and wood products, other forms of disturbances including conversion of mangrove areas for other uses including aquaculture and development particularly in urban areas have recently been cited as the major responsibles of mangrove degradation (Mukherjee *et al.*, 2014). Increased pressure in the catchment areas coupled with the predicted impacts of climate change may also just be a time bomb in waiting. Drawing inference from the C-S-R triangle (Grime *et al*., 1988) and the ball and cup analogy (Beisner *et al*., 2003), the results of this dissertation show that under incidences of disturbance, mangroves may remain in one stable state as individuals or as a community but this follows either or both anatomical and morphological adjustments.

From the structural survey done in Mtwapa Creek (Chapter 3), the results suggests that although the mangrove forest had high stem density and that the cover change analysis between the years 2000 and 2010 showed increase in cover, the argument by Koedam and Dahdouh-Guebas (2009) and Kairo *et al*. (2002) that ecological quality changes precede quantity changes cannot be ignored in this case. Mtwapa Creek mangroves may appear well stocked in terms of stand density but the characteristic low basal area observed could be an attribute of degradation (Bosire *et al*., 2013) hence possible loss of functionality. Moreover the basal area values are not comparable to most of the forest patches studied along the Kenyan coast (Kairo *et al.*, 2002; Kairo *et al.*, 2008) including the nearby peri-urban mangrove forest of Tudor Creek (Mohamed *et al.*, 2009).

The observed stunted *C. tagal* and conspicuous absence of the landward *A. marina* zone in most sections of the forest could also be associated with features of floristic shifts. In other mangrove patches along the Kenyan coast, *A. marina* occupies such areas (Kairo, 2001) and may also display double zonation (Dahdouh-Guebas *et al.*, 2004a). Our results from the socio-economic survey also revealed concerns by the local communities over the structural status of the forest characterised by absence of poles suitable for construction as well as reduced fish catch in the creek (over a period of 10 years before this study). As per the secondary data obtained by this study (Chapter 4), it is clear that illegal harvesting of mangroves is rampant in Kilifi county and this selective logging (e.g. poles of a particular size) could have greatly affected the stability of Mtwapa Creek mangrove forest as also witnessed in nearby Tudor Creek by Mohamed (2008). While some of the members of the local community have come up with alternative means of livelihood including mariculture and bee keeping in the mangrove areas to curb overexploitation (Okello *et al.*, 2012), it would also be of more value to consider the effect of such activities on the already degraded forest. Sedimentation was not viewed or at least not established as a problem to the mangroves of Mtwapa Creek currently. However, poor farming practises involving tilling close to the creek including slopes facing the mangroves could expose the forest to future deterioration as a result of sedimentation and mangrove burial as has been witnessed in Tudor Creek (Mohamed, 2008).

Plate 7.1 Galleys on slopes facing the mangrove area at Tudor Creek and terraces on agricultural farms to reduce chances of sediment being washed away (Source: Mohamed 2008)

8.3 Resilience of mangroves under instantaneous large sedimentation

We investigated the effect of partial burial on three mangrove tree species, *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*, through experimental sedimentation in three levels 15, 30 and 45 cm (Chapter 5, 6 and 7). In table 8.1 and figure 8.2, a summary of the main results in the three chapters is provided. While some of the observations specifically on root and bark development as well as hydraulic conductivity in partially buried trees were common across all species, all the three species studied displayed varying levels of sensitivity to partial burial.

The rather rapid responses at a time scale of less than 2 years observed upon burial signify a high plastic growth in response to sedimentation and hence demonstrated resilience capacity of mangroves to extreme conditions. This is in tandem with the fact that, plants unlike most animals maintain plasticity in growth during their entire developmental cycle and are thus able to adapt to fluctuations within their environment (Nicoll and Ray, 1995; Jain and Minocha, 2000). Such modular plasticity may enable plants to adapt and survive unfavourable and/or unexpected fluctuations in conditions of their environment. Plasticity may be initiated by different environmental drivers including: flooding (Yáñez-Espinosa *et al.*, 2008; Xiao *et al.*, 2010), sediment burial (Xu *et al.*, 2013) and shade (Stamm and Kumar, 2010), and may occur in various systems ranging from dunes (Xu *et al.*, 2013) over agricultural crops (Vidoz *et al.*, 2010) to marine plants (Schmitz *et al.*, 2006; Yáñez - Espinosa *et al.*, 2008; Xiao *et al.*, 2010).

When mangrove aerial roots (which function as breathing structures) are covered by sediment, as in our experiment, it was possible that gaseous exchange with the atmosphere is slowed down since the solid matrix of soils occludes the diffusion path of oxygen (Armstrong and Drew, 2002) and presence of organic material may further contribute to hypoxia. Such conditions limiting oxygen availability to the roots below the ground may interfere with physiological processes including root metabolism (Drew, 1997) and hence water and nutrient uptake by the roots (Smit and Stachowiak, 1988; Else *et al.*, 1995). In response, trees undergo diverse morpho-anatomical adjustments which are mainly regulated by phytohormones through integration of environmental inputs into a complex signalling network (Stamm and Kumar, 2010). In the current study an increase in aerial root density upon subjection of the three mangrove tree species to partial burial simulating sedimentation levels of 15, 30 and 45 cm was observed (Chapter 6). This suggests resource reallocation to support the roots, a phenomenon which has also been observed in dune plants after burial (Gilbert and Ripley, 2008). It may also suggest prioritisation in distribution of photoassimilates to the roots to cater for reduced metabolism hence facilitating the increased growth/ increase in biomass of the buried aerial roots observed (Zamski and Schaffer, 1996; Niu *et al*., 1998). As a result, not only new roots were produced but the original roots were able to remain alive. However, since different parts of the plants work in synergy, the functioning of one trait depends greatly on the other (Huber *et al.*, 2012). Plants may thus display trade off scenarios among various development processes such as, shoot elongation against root development (Xu *et al.*, 2013), leaf gain/ sizes versus reproduction including sacrificing less important smaller branches by limiting sapflow to crucial parts in times of water crisis (Zimmermann, 1983). Limited sapflow in branches following burial could not be categorically proven from the hydraulic conductivity tests (Chapter 6). However, the death of more branches in partially buried *C. tagal* trees tends to suggest such a reaction (Rowland *et al*., 2015). Additionally, an increased root growth (Chapter 7) at the expense of shoot elongation (Chapter 5) is observed.

In Chapter 5, crown foliage dynamics of three mangrove tree species exposed to three different levels of experimental partial burial were monitored over a period of one year. In *A. marina*, the trees produced more leaves during the wet season and less during the dry season. These results affirm the fact that seasonal variability exist in 'sink strengths'[▲] during plant development cycle (Zamski and Schaffer, 1996). The position of *A. marina* plots (Figure 5.1 in Chapter 5) in an area with shorter hydroperiod of flooding meant that the addition of more sediment made the trees even more reliant on rainfall. As a result, the trees only experience luxurious growth during the wet season and at that time root growth and leaf production could occur at the same time. Moreover, pneumatophores already appeared above the sediment after 6 months of burial thus taking up for the role of aeration. As a result, *A. marina* was able to maintain the phenological cycle while experiencing increased leaf emergence due to nutrient associated with terrestrial sediment input (Ellis *et al.*, 2004). *Ceriops tagal* is known to be a slow growing species (Okello, 2008), the first new aerial roots in the 15 and 30 cm sedimentation levels were observed above the new ground level after 11 months and after 13 months in the 45 cm level. Moreover, due to the morphology of the species, all the aerial roots were covered even at the lowest sedimentation treatment level. This explains the mortality and increased leaf loss observed in the species during the first quarter of the experiment. *Rhizophora mucronata* is known to be highly resistant to hypoxic conditions (Twilley *et al.*, 1996) as a result the trees maintained phenological dynamics as those of the controls even with partial burial. The morphology of the roots meant that a certain percentage of the roots are left even at 45 cm sedimentation level.

[▲] Sink strength is a term used to describe a plant organ's competitive ability to attract photoassimilates.

8.4 Higher or maintained hydraulic conductivity in partially buried mangroves, is it a norm?

In Chapter 6 of this study, the effect of partial burial on xylem structure and hydraulic conductivity of mangrove trees was evaluated after 14 months of exposure. A higher conductivity was observed in the 15 cm to 30 cm and even at 45 cm the values were either similar to controls (*A. marina* and *R. mucronata*) or higher (*C. tagal*). Plasticity in development was also observed in this part of the study as branches from partially buried trees showed development of features including higher vessel grouping, increased conductive area and lower total stomata area in the new leaves. Based on these observations, we suggest the following possible explanations to the hydraulic conductivity trends observed:

1) The more compact a sediment is, the smaller the pores and although greater tension is required to pull water here, such soils can maintain conductance longer (McDowell *et al*., 2008). The addition of a 'sediment pack' above the original ground level during the experiment meant more weight applied hence compacting the soil. As a result the soils could maintain conductance longer after the tides and during the neap tides when the areas were not inundated particularly in *A. marina*. This could have as well contributed to the observed hydraulic conductivity trends with burial. In addition, the production of fine adventitious roots with burial (Chapter 7) has also been shown to help compensate for reduced hydraulic conductivity of sediment (Ewers *et al.*, 2000). Since spontaneous benthic fauna such as crabs were allowed to colonise, soil can gradually develop channels through burrowing activity.

2) Increased difficulty in water absorption, may pose challenge in refilling of embolised vessels (McDowell, 2011). However, studies have also shown that refiling of embolised vessels can also be through phloem uploading (Nardini *et al.*, 2011). Embolism triggers the surrounding living cells to secrete solutes into the vessel creating an osmotic gradient which encourages the withdrawal of water from the adjacent fibers and parenchyma cells into the vessel (Brodersen, 2011). The observed increased thickness of bark tissue in this study (Chapter 7) as also seen in flooded trees has been associated with accelerated proliferation of phloem parenchyma cells (Kozlowski, 1997). This could have contributed to ease of refilling vessels, hence high hydraulic conductivity.

3) *Avicennia* is known to possess vessel characteristics that favour safety against cavitation (Robert *et al.*, 2009a). As a result, the additional feature produced due to partial burial (e.g. increased vessel grouping, adventitious roots, increased bark tissue), only acted to enhance

hydraulic conductivity. Moreover, *A. marina* has internal phloem (Schmitz *et al.*, 2008; Robert *et al.*, 2011) which means an increased phloem to xylem ratio, which could have enhanced its role in xylem repair, as also suggested by Salleo *et al.* (2004), Salleo *et al.* (2009) and Robert *et al.* (2011). Trees that maintain narrow hydraulic safety margins are on the other hand more prone to cavitation (Pockman and Sperry, 2000; Meinzer *et al.*, 2009a). These trees have a higher xylem water potential causing 50% loss of conductivity (Ψ_{50}) and to compensate for the low cavitation resistance, they possess higher recovery performance via vessel refilling (Ogasa *et al*., 2013). This could explain the sapflow patterns observed in *R. mucronata* and *C. tagal* even upon experimental sedimentation.

4) The increased root growth and changes in root anatomy particularly of the breathing roots (Chapter 7) prove the limitation of gaseous exchange by aerial roots under burial and the need for developing fast to cater for remediation. This could have effectively translated to the observed high water conductivity in the partially buried trees as in the process other adaptive mechanisms were also initiated to ensure sap flow.

5) Under water-limited conditions, plants can limit sapflow to only the most vulnerable or crucial parts by confining cavitation to the more expendable parts (Zimmermann, 1983). The observed leaf shedding and branch mortality in *C. tagal* while it maintains hydraulic conductivity could be as a result of the need to save parts which the tree has invested carbon in for longer periods of time. In times of drought stress for instance, walnut trees may reduce maximum hydraulic conductivity in petioles up to 6 times that in the stem (Tyree *et al.*, 1993).

8.5 Role of nutrients and crab burrowing in partially buried mangroves

Tides have been noted to play a significant role in distribution of free and particle-bound nutrients (Ball, 1988). However, mangrove sediments are still generally P-limited in less inundated areas, and N-limited in frequently inundated sites (Ball, 1988). As a result, any small input of nutrients could lead to a strong growth response (Lovelock *et al.*, 2004). Sedimentation particularly from terrigenous sources is associated with nutrient input (Ellis *et al.*, 2004; Alongi *et al.*, 2005) resulting in a positive growth response which has been expressed differently among the species studied. Moreover nutrient addition has been shown to act only as a secondary factor in contributing to increased tree growth in sites characterised by high sedimentation rates (Lovelock *et al.*, 2007), and when in excess may in fact result in exaggerated growth of shoot relative to the roots thus increasing vulnerability to drought events (Lovelock *et al.*, 2009). As a result the positive growth response including higher fecundity in *R. mucronata*, increased leaf flushing in *A. marina* that was observed in this study could be attributed to sedimentation with some degree of certainty.

Crabs are known to construct their burrows on the mangrove forest floor and in the process they change surface topography, particle size distribution and improve sediment aeration and, hence, reduce concentration of phytotoxins in the substratum (Smith III *et al.*, 1991; Botto and Iribarne, 2000). Phytotoxic compounds particularly sulphides (e.g. hydrogen sulphide) have a damaging effect on the root cell membranes and have been shown to negatively affect photosynthesis (Youssef and Saenger, 1998). As a result, crabs could significantly and positively affect growth and production of the mangrove trees (Smith III *et al.*, 1991; Smith *et al.*, 2009) as well as survival of seedlings (Youssef and Saenger, 1998), though herbivorous species can damage propagules, seedlings or trees (Clarke and Kerrigan, 2002; Dangremond, 2015; Van Nedervelde *et al*., 2015). Despite covering all burrows within each of the sedimentation plots at the beginning of the experiment, new burrows were formed at the new sediment level and species belonging to the dominant crab genera *Uca* and *Sesarma*, could be observed. This could have facilitated maintenance of sediment conditions as in the controls. Moreover, burrowing may also help maintain salinity at relatively low levels (Smith *et al.*, 2009).

8.7 Survival of the fittest- mortality among *C. tagal* trees under experimental partial sediment burial

The precise identification of the physiological mechanism that fails resulting in death of trees still remains a challenge (McDowell, 2011). After highlighting all the above mechanisms that could have been involved upon experimental partial burial, it is clear that the three common and biogeographically wide ranging mangrove tree species can adjust their morpho-anatomic features to grow better as though such disturbance does not signify stress, at least within the timeframe of observation under the conditions observed or imposed. From our results where trees survived up to 45 cm sedimentation level, it even becomes more unclear what caused diebacks in the mangroves documented by Ellison (1998) and why some of the *C. tagal* trees in our experiments died. We appreciate the difficulty in testing effects of individual factors under field conditions and that many other factors not accounted for in this study might have contributed to the observations made. Our results nevertheless suggest that the mortality observed in the work of Ellison (1998), after burial events in which various mangrove tree species including *A. marina* suffered dieback, may have not been solely as a result of sedimentation but rather the combination effect of waterlogging and sedimentation.

The results of this study clearly show that only trees that did not produce new aerial roots died. It thus follows that although *C. tagal* may not always possess well developed aerial roots (Tomlinson, 1994), development of this feature ensured survival after instantaneous large sedimentation in this particular experiment. Intraspecific variations may however, mean that some individual trees are not sufficiently plastic to adjust to environmental fluctuations thus succumb to change. In addition there are local differences which were observed leading to more branch drying in seaward plots as opposed to the landward plots (differing in flooding period). Such differences may exist regionally meaning that trees of the same species may suffer similar burial levels but experience dieback in one area but not in the other (Ellison 1998). Deaths observed in this study may also be explained through the loop effect suggested by McDowell (2011). An initial difficulty in water absorption, may pose a challenge in refilling of embolised vessels which may then lead to reduced photosynthetic capacity of affected trees. As a result the trees may have to mobilise the non-structural carbohydrates for use in respiration, growth and defence. Ultimately this leads to carbon starvation and eventually death.

8.8 Own perspective

In the work I presented, data are shown which indicate the resilience and short period adaptability of several young mangrove trees of three common and wide ranging species to sudden and heavy sedimentation. I do not intend to extrapolate this as yet such as to state that natural and expected major anthropogenic flooding and sedimentation events can be borne by mangroves in general. As I also observed and as has been corroborated by data from our research group elsewhere and in other settings by several authors, mangroves have suffered from sedimentation. Any such work as the one I performed with my colleagues is reductionist in nature, it necessarily narrows down to several factors, controlling for confounding factors and processes. However, *in situ* mangroves are not solely affected by sedimentation, but face a variety of impacts, many of them increasing due to human action. These combined factors may challenge the resilience of individual trees and the assemblage and ultimately the ecosystem and demand both the combination of reductionist approaches as well as comprehensive observations.

8.9 Areas for future research

All results in the present work must be considered within the framework of the assumptions and the experimental conditions imposed. While giving often clear patterns, it must be borne in mind that for full extrapolation or for assessing the general nature of our conclusions, the following could be thought of.

- While growth in plants may be a well-coordinated process, the partially buried trees showed some degree of investment in formation of new roots. This shift in biomass allocation could influence radial growth negatively (Anten *et al.*, 2009). Future studies should therefore focus on comparing the shoot-root ratio of affected trees which may help explain the high stem density with low basal area observed in Mtwapa Creek. Such studies should also take in to account ideas by Poorter and Nagel (2000) that plants allocate biomass in such a way as to maximise growth under any environmental condition. This may in the end open up insights into how much mangroves are able to give up in terms of growth to ensure 'escape' from a condition that is threatening survival.
- Though sedimentation is frequently observed in mangrove areas and also in Kenyan formation, changing patterns of currents and deposition also show root systems which are exposed, sometimes in proximity to sedimentation sites. Coastal erosion is a threat and mangroves may shield from coastal erosion if they can adapt. Preliminary and non-structured observations indicate that *Avicennia* spp. with its plastic growth appears to cope with exposure. Response to root exposure is worth investigating for mangrove trees in view of environmental change and ecosystem services.
- Phytohormones are responsible for regulating virtually all processes involved in plant growth (Wolters and Jϋrgens, 2009; Khan *et al.*, 2012). Ethylene specifically has been found to accumulate in plant tissues when submerged under waterlogged conditions (Visser *et al.*, 1996; Jackson *et al.*, 2003; Vidoz *et al.*, 2010). This hormone has been suggested to be responsible for incremental bark growth (Savidge, 1988) and adventitious root growth in *Rumex* plants (Visser *et al.*, 1996) under flooding. Our results show up to 4 fold increase in growth of bark tissue when buried and proliferous production of adventitious roots upon burial. Since phytohormones may be part of a larger chain of signal transduction and may work not only to regulate physiological processes but also each other (Machăčkovă and Romanov, 2002; Khan

et al., 2012), it would be prudent that the role of hormones and their interactions during burial stress mangrove trees be assessed further.

- We observed colonisation by higher inundation class mangrove species (*Lumnitzera racemosa*) in the 45 cm sedimentation plots of *R. mucronata*. This suggests that while mangroves may have the capacity to adapt and survive large sedimentation events, changes in hydrological regimes associated with large sediment input may lead to a complete floristic shift in the affected areas. In the process, some species may disappear and be replaced by new ones. Most striking were the terrestrial plants which were also observed to emerge in the sedimentation experimental plots, including *Casuarina equisetifolia* (exotic terrestrial species) and perennial grasses. Since these species either grow into large trees or full ground coverage they may out-compete mangroves in suboptimal conditions for these specialised trees (as can be observed in landward mangrove fringes). This information was not included in the main thesis document but it would be of great interest to dig further on the issue of floristic succession upon sedimentation and make long term observations to ascertain the effects and its transitional or lasting character.
- Studies have also suggested that plastic responses by plants to environmental fluctuations may be pronounced during initial exposure but constrained by subsequent similar change (Weinig and Delph, 2001). This may significantly affect resilience of systems to disturbance. Future studies should focus on repeated burial after selected period of time to ascertain this fact and evaluate the effect on the same growth variables studied currently.

In addition, I appreciate various loopholes in the current study but which could form important openings for suggestion on various measures to be taken in conducting a similar experiment in future. Personal evaluation of the study revealed the following limitations:

- The different times of establishment of the sedimentation experimental plots mean that the burial experiment did not run concurrently for the three species making comparison across species impossible due to the mixed time/treatment effects. The arguments would have been clearer for all traits if the experiments were set at the same time.

- The setup of the sediment burial experiment does not allow the disentangling of confounding effects like compaction, hypoxia and nutrient enrichment on the mangrove tree anatomy and hydraulic conductivity.
- Other than comparison between dead and surviving trees based on root development, anatomical comparison between the two would have also given further suggestion on the cause of death.
- The period of exposure and data collection in the burial experiment was too short to allow conclusive remarks regarding long term effect of sedimentation
- In the socio-economic survey, most of the respondents were men thus resulting in some form of gender bias

Table 8.1 Summary of effects of experimental partial burial mimicking three sedimentation levels (15, 30 & 45 cm) in mangrove tree species. Phenology data was collected over a period of one year after burial; Hydraulic conductivity, xylem structure and stomatal properties after 14 months; Root growth observed over 16 (*R. mucronata*), 22 (*A. marina*) and 26 (*C. tagal*) months after which final observations for bark and roots were made upon digging out trees. Data and observations are in reference to control trees

		Ceriops tagal		
Trait	***Avicennia marina***	Landward	Seaward	***Rhizophora mucronata***
Leaf emergence	Increase in wet season and decrease in dry season	Lower at 45 cm during first 3 quarters	Lower at 45 cm level only during second quarter	N.s.
Leaf loss	Higher during dry season	More during first quarter	More during first quarter	N.s.
Reproduction	Higher fecundity at all levels	N.s.	N.s.	Higher fecundity at 15 cm level
Leaf area	Maximum at 30 cm level	Reduced at 45 cm level	Reduced at 45 cm level	Maximum at 30 cm level
Shoot elongation	Higher	N.s.	N.s.	Higher only at 15 cm
Hydraulic conductivity	Higher at 15 & 30 cm levels	Higher at 15 & 30 cm levels	Higher at all levels	Higher at 15 & 30 cm levels
Xylem structure	Wider vessels, Higher conductive area, VGI* highest at 15 & 30 cm	Narrower vessels (least at 30 cm with high VGI*)	Wider vessels*, lower VGI	Wider vessels, higher VGI* maximum at 30 cm
Stomata area	N.s.	lower*	lower*	N.s.
Mortality	None	30.0% of the trees died at 45 cm	28.6% of trees died in the 45 cm	None
New roots & adventitious roots	All buried trees	Trees that died did not produce roots	Trees that died did not produce roots	All buried trees
Bark	Thicker in portion buried below sediment	Thicker in portion buried below sediment	Thicker in portion buried below sediment	Thicker in portion buried below sediment

N.s. = partially buried trees similar to controls; VGI=Vessel grouping index; *are features which could explain the observed hydraulic conductivity patterns

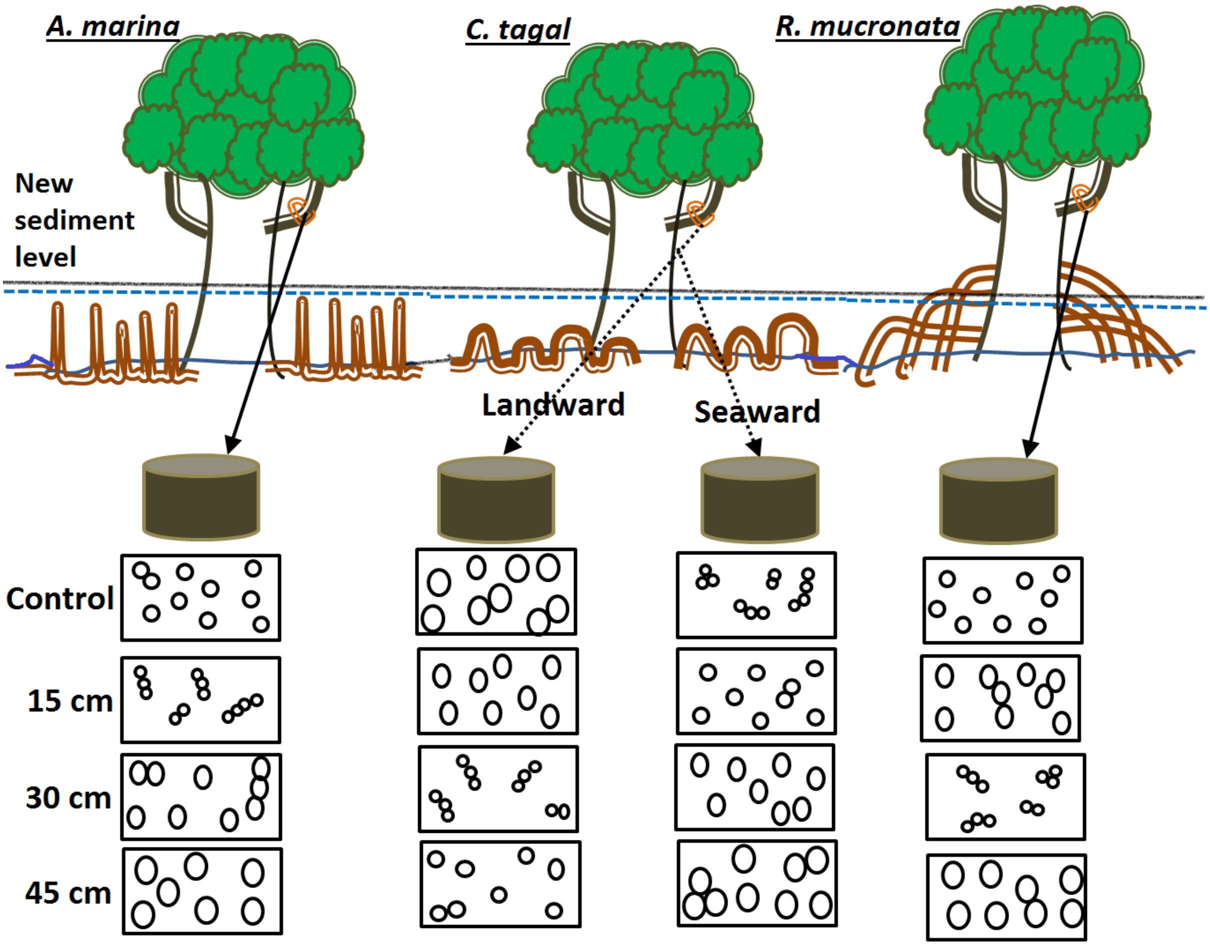


Figure 8.2 A diagrammatic and schematised representation of vessel characteristic in the three mangrove tree species *A. marina*, *C. tagal* and *R. mucronata* following 14 months of partial sediment burial of 15, 30 and 45 cm. The representation indicates (1) vessel density, (2) vessel grouping and (3) vessel size.

PART V

References and appendices

References

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

Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murray, J., Sala, O.E., 2008. Mangroves in the Gulf of California increase fishery yields. Proceedings of the National Academy of Sciences USA, USA 105:10456-10459.

Aksornkoae, S., 1993. Ecology and management of mangrove. In, IUCN - The World Conservation Union, Bangkok, Thailand, p. 176.

Alemán , M.I., Bourgeois, C., Appeltans, W., Vanhoorne, B., De Hauwere, N., Stoffelen, P., Heughebaert, A., Dahdouh-Guebas, F., 2010. The 'Mangrove Reference Database and Herbarium' MRDH. Plant Ecology and Evolution 143, 225-232.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259, 660-684.

Allen, J.A., Ewel, K.C., Jack, J., 2001. Patterns of natural and anthropogenic disturbance of the mangroves on the Pacific Island of Kosrae. Wetlands Ecology and Management 9, 279-289.

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., 2009. The energetics of mangrove forests. Springer Science + Business Media B.V., Townsville, Queensland, Australia.

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.

Alongi, D.M., Sasekumar, A., Chong, V.C., Pfitzner, J.T., L.A., Tirendi, F., Dixon, P., Brunskill, G.J., 2004. Sediment accumulation and organic material flux in a managed mangrove ecosystem: Estimates of land-ocean-atmosphere exchange in peninsular Malaysia. Marine Geology 208, 383-402.

Anten, N.P.R., Von Wettberg, E.J., Pawlowski, M., Huber, H., 2009. Interactive effects of spectral shading and mechanical stress on the expression and costs of shade avoidance. The American Naturalist 173, 241-255.

Archibold, O.W., 1995. Ecology of world vegetation. Chapman & Hall, London.

Armstrong, W., Drew, M.C., 2002. Root growth and metabolism under oxygen deficiency. In: Waisel, Y., Eshel, A., Kafkafi, U. (Eds.), Plant Roots: the hidden half (3rd Edition). Marcel Dekker, New York & Basel, pp. 729-761.

Arthurton, R.S., 1992. Beach erosion: case studies on the East African coast. In, Bordomer 92, International Convention on Rational Use of Coastal Zone, Intergovernmental Oceanographic Commission, Bordeaux, pp. 91-95.

Awad, H., Barigah, T., Badel, E., Cochard, H., Herbette, S., 2010. Poplar vulnerability to xylem cavitation acclimates to drier soil conditions. Physiol Plantarum 139, 280-288.

Ball, M.C., 1980. Patterns of Secondary Succession in a Mangrove Forest of Southern Florida. Oecologia 44, 226-235.

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

Ball, M.C., Canny, M.J., Huang, C.X., Egerton, J.J.G., Wolfe, J., 2006. Freeze/thaw-induced embolism depends on nadir temperature: the heterogeneous hydration hypothesis. Plant Cell and Environment 29, 729-745.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, S.J., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K., Turner, R.K., 2002. Economic reasons for conserving wild nature. Science's Compass 297, 950-953.

Bamroongrugsa, N., Yuanlaie, P., 1995. Mangrove afforestation on newly formed mudflats of Patani Bay, Southern Thailand. In: Khemnark, C. (Ed.), Ecology and management of mangrove restoration and regeneration in East and South East Asia. Proceedings of the ECOTONE IV, 18-22 January 1995, Bangkok, pp. 230-238.

Bann, C., 1999. A contingent valuation of the mangroves of Benut, Johor State, Malaysia. Johor State Forestry Department/ DANCED/ Darudec, pp78.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services: Reviews. Ecological Monographs 81, 169-193.

Beck, C.B., 2010. Periderm, rhytidome, and nature of bark. In: Beck, C.B. (Ed.), An introduction to plant structure and development: plant anatomy for the twenty-first century (Second edition).

Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. Front Ecol Environ 7, 376-382.

Betagoda, B.M., 2003. The economic valuation of alternative uses of mangrove forests in Sri-Lanka. UNEP/Global Programme of Action for Protection of the Marine Environment from Land-based Activities, The Hague.

Bhosale, L.J., Mulik, N.G., 1991. Proceedings. In, international seed symposium, Jodhpuur, India.

Blasco, F., Saenger, P., Janodet, E., 1996. Mangroves as indicators of coastal change. Catena 27, 167-178.

Böer, B., 1993. Anomalous pneumatophores and adventitious roots of *Avicennia marina* (Forsk.) Vierh. mangroves 2 years after the 1991 Gulf-war oil-spill in Saudi-Arabia. Marine Pollution Bulletin 27, 207-211.

Borkar, M.U., Athalye, R.P., Goldin, Q., 2009. Salinity induced changes in the leaf anatomy of mangrove *Avicennia marina* along the anthropogenically stressed tropical creek. Journal of Coastal Development 14, 191-201.

Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Koedam, N., 2003. Colonization of non-planted mangrove species into restored mangrove stands in Gazi Bay, Kenya. Aquatic botany 76, 267-279.

Bosire, J., Dahdouh-Guebas, F., Kairo, J.G., Wartel, S., Kazungu, J., Koedam, N., 2006. Success rates of recruited tree species and their contribution to the structural development of reforested mangrove stands. Marine Ecology Progress Series 325, 85-91.

Bosire, J., 2006. Ecological recovery of reforested mangroves in Kenya. Dissertation, Vrije Universiteit Brussels, Belgium.

Bosire, J., Kairo, J.G., 2008. Research for sustainable mangrove management in Kenya. A magazine of the Department of Fisheries of Kenya, pp 47-49.

Bosire, J., Kaino, J.J., Olagoke, A.O., Mwihaki, L.M., Ogendi, G.M., Kairo, J.G., Macharia, D., 2013. Mangroves in peril: unprecedented degradation rates of peri-urban mangroves in Kenya. Biogeosciences 10, 16371-16404.

Bosire, J., Kiplagat, J., Mironga, J., Ogendi, G., Mugi, L., Mbelase, A., 2015. Landscape assessment of mangrove ecosystem integrity. 9th Western Indian Ocean symposium, University of Kwazulu-Natal, South Africa.

Botto, F., Iribarne, O., 2000. Contrasting effect of two burrowing crabs (*Chasmangnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. Estuarine Coastal and Shelf Science 51, 141-151.

Bouillon, S., Borges, A.V., Castaneda-Moya, E., Diele, K., Dittmar, T., Duke, N.C., Kristensen, E., Lee, S.Y., Marchand, C., Middelburg, J.J., Rivera-Monroy, V.H., Smith III, T.J., Twilley, R.R., 2008. Mangrove production and carbon sinks: A revision of global budget estimates. Global Biogeochemistry Cycles 22, GB2013.

Bradley, B.W., 2005. Ecological effects of small scale cutting of Philippine mangrove forests. Forest Ecology and Management 206, 331-348.

Brodersen, C.R., 2011. Automated analysis of three-dimensional xylem networks using high-resolution computed tomography. not yet online.

Brodersen, C.R., McElrone, A.J., Choat, B., Matthews, M.A., Shackel, K.A., 2010. The Dynamics of Embolism Repair in Xylem: In Vivo Visualizations Using High-Resolution Computed Tomography. Plant Physiology 154, 1088-1095.

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

Brooks, J.R., Angeles, G., Bond, B., Boya, J.S., Brodibb, T., Burns, M.J., 2004. The Cohesion-Tension Theory: letter. New Phytol. 163, 451-452.

Brown, T., Schneider, H., Harper, D., 1996. Multi-scale estimates of erosion and sediment yields in the Upper Tana basin, Kenya. Erosion and Sediment Yield: Global and Regional Perspectives (Proceedings of the Exeter Symposium, July), IAHS Publ. no. 236.

Bunce, L., Townsley, P., Pomeroy, R., Pollnac, R., 2000. Socioeconomic manual for coral reef management. Australian Institute of Marine Science, 92-168.

Bunt, J.S., Stieglitz, T., 1999. Indicators of mangrove zonality: the Normanby River, North East Australia. Salt marshes 3, 177-184.

Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M., Cerabolini, B., 2006. The functional basis of a primary succession resolved by C-S-R classification OIKOS 112, 10-20.

Cahoon, D.R., Hensel, P., 2002. Hurricane mitch: A regional perspective on mangrove damage, recovery, and sustainability. In. U.S. Department of Interior Geological surveys, USGS Open file report 03-183, p. 31.

Cahoon, D.R., Lynch, A.M., 1997. Vertical accretion and shallow subsidence in a mangrove forest of South western Florida, U.S.A. Mangr. Salt Marsh 1, 173-186.

Caldeira, K., 2012. The great climate experiment: How far can we push the planet? Scientific American (September) 307, 64-69.

Camacho-B, S.E., Hall, A.E., Kaufmann, M.R., 1974. Efficiency and regulation of water transport in some woody and herbaceous species. Plant Physiology 54, 169-172.

Cancino, J., Von Gadow, K., 2002. Stem number guide curves for uneven-aged forests – development and limitations. In: Von Gadow, K., Nagel, J., Saborowski, J. (Eds.), Continuous cover forestry. Kluwer Academic Press, Dordrecht, pp. pp 163-174.

Carlquist, S., 2009. Xylem heterochrony: an unappreciated key to angiosperm origin and diversifications. Botanical Journal of the Linnean Society 161, 26-65.Carlquist, S., 2001. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood, 2nd Edition. Springer Verlag, Berlin.

Carlquist, S., 1984. Vessel grouping in dicotyledonous wood: significance and relationship to imperforate tracheary elements. Aliso 10, 505-525.

Cerón-Bretón, R.M., Cerón-Bretón, J.G., Sánchez-Junco, R.C., Damián-Hernández, D.L., Guerra-Santos, J.J., Muriel-Garcia, M., Cordova-Quiroz, A.V., 2011. Evaluation of carbon sequestration potential in mangrove forest at three estuarine sites in Campeche, Mexico. International Journal of Energy and Environment 5.

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.

Choat, B., Lahr., E.C., Melcher, P., 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.

Choong, M.F., Lucas, P.W., Ong, J.S.Y., Pareira, B., Tan, H.T.W., Turner, I.M., 1992. Leaf fracture toughness and schelerophylly: their correlations and ecological implications. New Phytol. 121, 597-610.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A., Whetton, P., 2007. Regional climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 926.

Christman, M.A., Sperry, J.S., 2010. Single-vessel flow measurements indicate scalariform perforation plates confer higher flow resistance than previously estimatedpce_2094 1. Plant, Cell and Environment not yet online.

Christman, M.A., Sperry, J.S., Adler, F.R., 2009. Testing the 'rare pit' hypothesis for xylem cavitation resistance in three species of Acer. New Phytologist 182, 664-674.

Cicin-Sain, B., Belfiore, S., 2005. Linking marine protected areas to integrated coastal and ocean management: A review of theory and practice. Ocean & Coastal Management 48, 847-868.

Cinner, J.E., Pollnac, R.B., 2004. Poverty, perceptions and planning: why socioeconomics matter in the management of Mexican reefs. Ocean & Coastal Management 47, 479-493.

Cintrón, G., Schaeffer-Novelli, Y., 1984. Methods for studying mangrove structure. In: Snedaker, S.C., Snedaker, J.G. (Eds.), The mangrove ecosystem: research methods. UNESCO, Paris, France, pp. 91-113.

Clarke, P.J., 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in South eastern Australia. Aquatic Botany 45, 193-204.

Clarke, P.J., Kerrigan, R.A., Westphal, C.J., 2001. Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? Journal of Ecology 89, 648-659.

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

Clutter, J.L., Fortson, J.C., Pienaar, L.V., Brister, G.H., Bailey, R.L., 1983. Timber management: a quantitative approach. John Wiley and Sons.

Cochard, H., 2002. A technique for measuring xylem hydraulic conductance under high negative pressures. Plant, Cell and Environment 25, 815-819.

Cochard, H., 2006. Cavitation in trees. Comptes Rendus Physique 7, 1018-1026.

Colmer, T.D., 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots Plant Cell and Environment 26, 17-36.

Colmer, T.D., Voesenek, L.A.C.J., 2009. Flooding tolerance: suites of plant traits in variable environments. Functional Plant Biology 6, 665-681.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., al., e., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

Connell, J.H., Sousa, W.P., 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist 121, 789-824.

Costanza, R., Pérez-Maqueo, O., Martinez, l.M., Sutton, P., Anderson, S.J., Mulder, K., 2008. The value of coastal wetlands for hurricane protection. Ambio 37.

Corcoran, E., Ravilious, C., Skuja, M., 2007. Mangroves of Western and Central Africa. In. UNEP World Conservation Monitoring Centre, Cambridge, p. 92.

Coupland, G.T., Paling, E.I., McGuinness, K.A., 2005. Vegetative and reproductive phenologies of four mangrove species from Northern Australia. Australian Journal of Botany 53, 109-117.

Craine, J.M., 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of Ecology 93, 1041-1052.

Crawford, R.M.M., 1992. Oxygen availability as an ecological limit to plant distribution. Advances in Ecological Research 23, 93-185.

Crona, B., Rönnbäck, P., 2005. Use of replanted mangroves as nursery grounds by shrimp communities in Gazi Bay, Kenya. Estuarine Coastal and Shelf Science 65, 535-544.

Crona, B., Rönnbäck, P., 2007. Community structure and temporal variability of juvenile fish assemblages in natural and replanted mangroves, *Sonneratia alba* Sm., of Gazi Bay, Kenya. Estuarine, Coastal and Shelf Science 74, 44-52.

Cruiziat, P., Cochard, H., Améglio, T., 2002. Hydraulic architecture of trees: main concepts and results. Ann Forest Sci 59, 723-752.

Curtis, J.T., 1956. The vegetation of Wisconsin: An ordination of plant communities. University of Wisconsin Press, Madison, Wisconsin, USA.

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.

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

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

Dahdouh-Guebas, F., Van Pottelbergh, I., Kairo, J.G., Cannicci, S., Koedam, N., 2004b. Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on Retrospective remote sensing, social surveys, and distribution of trees. Marine Ecology Progress Series 272, 77-92.

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

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J., Lo Seen, D., Koedam, N., 2005b. How effective were mangroves as a defence against the recent tsunami? Current Biology 15.

Dahdouh-Guebas, F., Koedam, N., 2006. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): Solutions to ambiguous field situations and description of the PCQM plus protocol. Forest Ecology and Management 228, 1-18.

Dahdouh-Guebas, F., Kairo, J.G., De Bondt, R., Koedam, N., 2007. Pneumatophore height and density in relation to microtopography in the grey mangrove *Avicennia marina*. Belgian Journal of Botany 140, 213-221.

Dahdouh-Guebas, F., 2013. Les biens et services écosystémiques: l'exemple des mangroves. In: P. Meerts (ed.), *Vers une nouvelle synthèse écologique: de l'écologie scientifique au développement durable.* Centre Paul Duvigneaud de Documentation Ecologique, Bruxelles, Belgique: 182-193.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, E., Peterson, C., Simberloff, D., Swanson, F., Stocks, B., Wotton, M., 2001. Climate change and forest disturbances. BioScience 51, 723-734.

Dangremond, E.M., 2015. Propagule predation by crabs limits establishment of an endemic mangrove. Hydrobiologia 755, 257-266.

Dayton, P., Curran, S., Kitchingman, A., Wilson, M., Catenazzi, A., Restrepo, J., Birkeland, C., Blaber, S., Saifullah, S., Branch, G., Boersma, D., Nixon, S., Dugan, P., Davidson, N., Vorosmarty, C., 2005. Coastal Systems. In: Agardy, T., Alder, J. (Eds.), Ecosystems and human well-being: current status and trends. Millennium Ecosystem Assessment. Island press, Washington, pp. 513-550.

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 Deurwaerder, H., Okello, J.A., Schmitz, N., Koedam, N., Steppe, K., 2016. How are anatomical and hydraulic features of mangroves *Avicennia marina* and *Rhizophora mucronata* influenced by sedimentation. Trees DOI 10.1007/s00468-016-1357-x.

De Ryck, D.J.R., Robert, E.M.R., Schmitz, N., Van der Stocken, T., Di Nitto, D., Dahdouh-Guebas, F., Koedam, N., 2012. Size does matter, but not only size: Two alternative dispersal strategies for viviparous mangrove propagules. Aquatic Botany 103, 66-73.

de Silva, N.D.G., Cholewa, E., Ryser, P., 2012. Effects of combined drought and heavy metal stresses on xylem structure and hydraulic conductivity in red maple (*Acer rubrum* L.). Journal of Experimental Botany 63, 5957-5966.

Didham, R.K., Watts, C.H., Norton, D.A., 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? Oikos 110, 409-416.

Dixon, H.H., Joly, J., 1895. On the ascent of sap. Philosophical Transactions of The Royal Society of London 186, 563-576.

Domec, J.C., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., Villalobos-Vega, R., 2006. Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: impact on stomatal control of plant water status. Plant, Cell and Environment 29, 26-35.

Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurniato, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nature geoscience Letters.

Drew, J. A. (2005). Use of traditional ecological knowledge in marine conservation. Conservation Biology *19*, 1286-1293.

Drew, M.C., 1997. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Phys Plant Mol Biol 48, 223-250.

Drew, M.C., Jackson, M.B., Giffard, S., 1979. Ethylene promoted adventitious roots and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. . Planta 147, 83-88.

Drexler, J.Z., 2001. Maximum longevities of *Rhizophora apiculata* and *Rhizophora mucronata* propagules. Pacific Science 55, 17-22.

de Lacerda, L.D. (Ed.), 2002. Mangrove ecosystems: function and management. Springer-Verlag, Berlin Heidelberg

Ducey, M.J., unpublished. The reverse-J and beyond: developing practical, effective marking guides. In.

Duke, N.C., 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. . Wetlands Ecology and Management 9, 257-269.

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? Letters. Science 317, 41-42.

Ellegaard, M., Nguyen, N.T.G., Andersen, T.J., Michelsen, A., Nguyen, N.L., Doan, N.H., Kristensen, E., Weckström, K., Hoang Son, T.P., Lund-Hansen, L.C., 2014. Temporal changes in physical, chemical and biological sediment parameters in a tropical estuary after mangrove deforestation. Estuarine, Coastal and Shelf Science 142, 32-40.

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., 1996a. Anthropogenic disturbances in the Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica 28, 549-565.

Ellison, A.M., Farnsworth, E.J., 1996b. 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, A.M., Farnsworth, E.J., 1997. Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (Rhizophora mangle L.). Oecologia 112, 435-446.

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

Else, M.A., Davis, W.J., Malone, M., Jackson, M.B., 1995. A negative hydraulic message from oxygen-deficient roots of tomato plants? Influence of soil flooding on leaf water potential, leaf expansion, and synchrony between stomatal conductance and root hydraulic conductivity. Plant Physiology 109, 1017-1024.

Eusebio, M.A., Tesoro, F.O., Cabahug, D.M., 1986. Environmental impact of timber harvesting on mangrove ecosystem in the Philippines. In: Committee, N.M. (Ed.), Mangroves of Asia and the Pacific: Status and Management. Natural Resources Management Centre (NMRC), Ministry of Natural Resources, Quezon city, Philippines.

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

Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant, Cell and Environment 23, 1055-1066.

Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: a review and synthesis. Marine Pollution Bulletin 50, 125-146.

FAO, 1994. Mangrove forest management guidelines. Food and Agricultural Organisation of the United Nations, Rome.

FAO, 2007a. Coastal protection in the aftermath of the Indian Ocean tsunami: what role for forests and trees? Proceedings of Regional Technical Workshop, Khao Lak, Thailand, pp 213.

FAO, 2007b. Mangroves of Africa 1980-2005: Country Reports. In. Food and Agriculture Organization of the United Nations, Rome, p. 155.

FAO, 2007c. The world's mangroves 1980-2005, FAO forestry paper 153. In. Forest Resources Division, FAO, Rome, p. 77.

Feka, N.Z., Manzano, M.G., Dahdouh-Guebas, F., 2011. The effects of different gender harvesting practises on mangrove ecology and conservation in Cameroon. International Journal of Biodiversity Science, 1-14.

Feller, I.C., 1996. Effect of nutrient enrichment on leaf anatomy of dwarf *Rhizophora mangle* L. (red mangrove). Biotropica 28, 13-22.

Field, C.D., 1996. Restoration of mangrove ecosystems. International Society for Mangrove Ecosystems (ISME), Okinawa, Japan, 250.

Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. Science 296, 1689-1691.

Frank, C.F., 2014. Community participation in natural resources management: successes and failures in Mida Creek mangrove forest, Kenya. In, Faculty of Science and Bio-engineering Sciences. Vrije Universiteit Brussels, Brussels.

Friess, D.A., Krauss, K.W., Horstman, E.M., Balke, T., Bouma, T.J., Galli, D., Webb, E.L., 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biological Reviews 87, 346-366.

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

Gang, P.O., Agatsiva, J.L., 1992. The current status of mangrove along the Kenyan coast: a case study of Mida Creek mangroves based on remote sensing. Hydrobiologia 247, 29-36.

Gärtner, H., Lucchinetti, S., Schweingruber, F.H., 2014. New perspectives for wood anatomical analysis in Dendrosciences: the GSL1-microtome. Dendrochronologia 32, 47-51.

Gilbert, G.S., Mejía-Chang, M., Rojas, E., 2002. Fungal diversity and plant disease in mangrove forests: salt excretion as a possible defence mechanism. Oecologia 132, 278-285.

Gilbert, M.E., Ripley, B.S., 2008. Biomass reallocation and the mobilization of leaf resources support dune plant growth after sand burial. Physiol Plantarum 134, 464-472.

Gilman, E.L., Ellison, J.C., 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., Tieszen, Z.Z., Singh, A., Loveland, T., Masek, J., Duke, N.C., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecol. Biogeogr. 20, 154-159.

Githiomi, J.K., Oduor, N., 2012. Strategies for sustainable wood fuel production in Kenya. International Journal of Applied Science and Technology 2, 21-25.

Gitz, D.C., Baker, J.T., 2009. Methods for creating stomatal impressions directly onto archivable slides. Agronomy Journal 101, 232-236.

Gómez-Cadenas, A., Francisco, R.T., Talon, M., Primo-Millo, E., 1996. Leaf abscission induced by ethylene in water-stressed intact seedlings of *Cleopatra mandarin* requires previous abscisic acid accumulation in roots. Plant Physiology 112, 401-408.

Government of Kenya, 2015. National mangrove ecosystem management Plan. State Department of Environment and Natural Resources, pp 59.

Government of Kenya, 2007. Kenya atlas of our changing environment. United Nations Environmental Programme.

Government of Kenya, 2009. State of the coast report: Towards integrated management of coastal and marine resources in Kenya. National Environment Management Authority, Nairobi, 88.

Government of Kenya, 2010. The 2009 Kenya population and housing census: Counting our people for the implementation of vision 2030. Volume IC population distribution by age, sex and administrative units.

Government of Kenya, 2012. Independent Electoral and Boundaries Commission, Kenya: Final report of boundaries of constituencies and wards gazetted on 7-3-12.

Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. Biodiversity and Conservation 6, 153-175.

Grime, J. P. 1974. Vegetation classification by reference to strategies. _ Nature 250: 26_ 31.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological andevolutionary theory. _ Am. Nat. 111: 1169_ 1194.

Grime, J. P. 1979. Plant strategies and vegetation processes._ Wiley.

Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative plant ecology. Allen and Unwin. London. 742pp

Grime, J. P. 2001. Plant strategies, vegetation processes and ecosystem properties (2nd ed.). Wiley.

Grime, J. P. and Mackey, J. M. L. 2002. The role of plasticity in resource capture by plants. Evol. Ecol. 16: 299_ 307.

Gubelman, E., 2009. Devastating new port proposal for the Lamu Archipelago. In. Mangrove Action Project (MAP) news.

Gunawardena, M., Rowan, J.S., 2005. Economic valuation of a mangrove ecosystem threatened by shrimp aquaculture in Sri Lanka. Environ. Management 36, 535-550.

Hacke, U.G., 2015. Functional and ecological xylem anatomy. Springer International, Switzerland: ISBN 978-3-319-15783-2

Hacke, U.G., 2014. Variable plant hydraulic conductance. Tree Physiology 34, 105-108.

Hacke, U.G., Sperry, J.S., 2003. Limits to xylem refilling under negative pressure in *Laurus nobilis* and *Acer negundo*. Plant, Cell and Environment 26, 303-311.

Hacke, U.G., Sperry, J.S., 2001. Functional and ecological xylem anatomy. Perspectives in Plant Ecology, Evolution and Systematics 42, 97-115.

Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J., McCulloh, K.A., 2001. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. Plant Physiology 125, 779-786.

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.

Harty, C., 2009. Mangrove planning and management in New Zealand and South East Australia - A reflection on approaches. Ocean & Coastal Management 52, 278-286.

Hatton, J.C., Couto, A.L., 1992. The effect of coastline changes on mangrove community structure, Portuguese Island, Mozambique. Hydrobiologia 247, 49-57.

Hauff, R.D., Ewel, K.C., Jack, J., 2006. Tracking human disturbance in mangroves: estimating harvest rates on a Macronesian Island. Wetlands Ecology and Management 14, 95-105.

Hegazy, A., 1998. Perspectives on survival, phenology, litterfall and decomposition, and caloric content of *Avicennia marina* in Arabian Gulf region. Journal of Arid Environments 40, 417-429.

Hemminga, 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs of Gazi Bay, Kenya. Marine Ecology Progress Series 106, 291-301.

Henniges, Y., Vollmer, I., Weber, R.W.S., Go¨rgens, M., Chmielewski, F.M., 2007. Climate change, a challenge for the North German fruit growing: experimental releases of fruit ring of the Altes Land. 62, 147-151.

Herrera, A., 2013. Responses to flooding of plant water relations and leaf gas exchange in tropical tolerant trees of a black-water wetland. Frontiers in Plant Science 4.

Hewawassam, T., Von Blanckenburg, F., Schaler, M., Kubik, P., 2003. Increase of human over natural erosion rates in tropical highlands constrained by cosmogenic nuclides. Geology 31, 597-600.

Hodgson, J.G., Wilson, B.J., Hunt, R., Grime, J.P., Thompson, K., 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. Oikos 85, 282-294.

Hogarth, P.J., 2015. The biology of mangroves and seagrasses. Oxford University Press, Great Clarendon Street.

Holbrook, N.M., Zwieniecki, M.A., 1999. Embolism repair and xylem tension: Do we need a miracle? Plant Physiology 120, 7-10.

Horowitz, L.S., 2001. Perceptions of nature and responses to environmental degradation in New Caledonia. Ethnobiology 40, 237-250.

Hubbell, S.P., 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203, 1299-1309.

Huber, H., Chen, X., Hendriks, M., Keijsers, D., Voesenek, L.A.C.J., Pierik, R., Pooter, H., De Kroon, H., Visser, E.J.W., 2012. Plasticity as a plastic response: how submergence-induced leaf elongation in *Rumex palustris* depends on light and nutrient availability in its early life stage. New Phytol. 194, 572-582.

Hutchings, P., Saenger, P., 1987. Ecology of mangroves. Queensland University press, Brisbane.

Huxham, M., Kimani, E., Augley, J., 2004. Mangrove fish: a comparison of community structure between forested and cleared habitats. . Estuarine Coastal and Shelf Science 70, 1554-1567.

IEBC, 2012. Independent Electoral and Boundaries Commission, Kenya: Final report of boundaries of constituencies and wards gazetted on 7-3-12.

IPCC, 2007. Climate change synthesis report: an assessment of the Intergovernmental Panel on Climate Change. IPCC Plenary XXVII Valencia, Spain, 12-17 November.

IPCC, 2014. Climate change 2014: Impacts, adaptations, and vulnerability. Part B: Regional aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental panel on Climate Change. Cambrdge University Press, Cambridge UK and NY USA, pp. 1199-1265.

Ishshalomgordon, N., Dubinsky, Z., 1992. Ultrastructure of the pneumatophores of the mangrove *Avicennia marina* South African Journal of Botany 58, 358-362.

ITTO, 1993. The economic and environmental value of mangrove forest and their present state of conservation. Japan International Association for Mangroves and International Society for Mangrove Ecosystems.

Jackson, M.B., Armstrong, W., 1999. Formation of aerenchyma and the process of plant ventilation in relation to soil flooding and submergence. Plant Biology 1, 274-287.

Jackson, M.B., Fenning, T.M., Drew, M.C., Saker, L.R., 1985. Stimulation of ethylene production and gas-space (aerenchyma) formation in adventitious roots of *Zea mays* L. by small partial pressure oxygen. Planta 165, 486-492.

Jackson, M.B., Saker, L.R., Crisp, C.M., Else, M.A., Janowiak, F., 2003. Ionic and pH signalling from roots to shoots of flooded tomato plants in relation to stomatal closure. Plant Soil 253, 103-113.

Jacobsen, A.L., Agenbag, L., Esler, K.J., Pratt, R.B., Ewers, F.W., Davis, S.D., 2007. Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa. Journal of Ecology 95, 171-183.

Jain, S.M., Minocha, S.C., 2000. Molecular biology of woody plants, volume 1. Kluwer Academic Publishers, Netherlands.

Jansen, S., Choat, B., Pletsers, A., 2009. Morphological Variation of Intervessel Pit Membranes and Implications to Xylem Function in Angiosperms. American Journal of Botany 96, 409-419.

Jansen, S., Gortan, E., Lens, F., Lo Gullo, M.A., Salleo, S., Scholz, A., Stein, A., Trifilo, P., Nardini, A., 2011. Do quantitative vessel and pit characters account for ion-mediated changes in the hydraulic conductance of angiosperm xylem? New Phytologist 189, 218-228.

Janzen, D.H., 1985. *Spondias mombin* is culturally deprived in megafauna-free forest. Journal of Tropical Ecology 1, 131-155.

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

Jayatissa, L.P., Wickramasinghe, W.A.A.D.L., Dahdouh-Guebas, F., Huxham, M., 2008. Interspecific variations in responses of mangrove seedlings to two contrasting salinities. International Review of Hydrobiology 93, 700-710.

Johns, D.A., 1986. Effects of selective logging on behavioural ecology of West Malaysian primates. Ecology 67, 684-694.

Johnson, D.M., Sherrard, M.E., Domec, J.C., Jackson, R.B., 2014. Role of aquaporin activity in regulating deep and shallow root hydraulic conductance during extreme drought. Trees DOI 10.1007/s00468-014-1036-8.

Jones, H.G., Sutherland, R.A., 1991. Stomatal control of xylem embolism. Plant Cell and Environment 14, 607-612.

Junghans, U., Langenfeld-Heyser, R., Polle, A., Teichmann, T., 2004. Effect of auxin transport inhibitors and ethylene on the wood anatomy of poplar. Plant Biology 6, 22-29.

Kairo, J.G., 1992. Some human induced stresses on the mangrove ecosystems of Kenya. In. Mangrove mapping team, Forest Department, Nairobi.

Kairo, J.G., 1995. Artificial regeneration and sustainable yield management of mangrove forests in Gazi Bay, Kenya. . In, Botany. University of Nairobi, Nairobi, Kenya, p. 116.

Kairo, J.G., 2001a. Ecology and restoration of mangrove systems in Kenya. In, Mangrove ecology and silviculture. Vrije Universiteit Brussels, Brussels, Belgium.

Kairo, J.G., Dahdouh-Guebas, F., Bosire, J., Koedam, N., 2001b. Restoration and management of mangrove systems - a lesson for and from the East African region. South African Journal of Botany 67, 383-389.

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

Kairo, J.G., 2003. Kenya. In: Macintosh, D.J., Ashton, E.C. (Eds.), Report on the Africa regional workshop on the sustainable management of mangrove forest ecosystems. ISME/cen TER Aarhus, Washington, DC.

Kairo, J.G., Lang'at, J.K.S., Dahdouh-Guebas, F., Bosire, J., Karachi, M., 2008. Structural development and productivity of replanted mangrove plantations in Kenya. Forest Ecology and Management 255, 2670-2677.

Kairo, J.G., Wanjiru, C., Ochiewo, J., 2009. Net pay: economic analysis of replanted mangrove plantation in Kenya. Journal of sustainable Forestry 28, 395-414.

Kairu, K.K., 2003. Coastal erosion in Kenya: Malindi-Ungwana Bay case study. A report prepared for UNEP/ GPA/ UNEP and WIOMSA.

Kangas, P., 2002. Mangrove forest structure on the Sittee River, Belize. In. Natural Resource Management Program, University of Maryland.

Karunathilake, K.M.B.C., 2003. Status of mangroves in Sri Lanka. Journal of Coastal Development 7, 5-9.

Kathiresan, K., 2003. How do mangrove forests induce sedimentation? Revisita de biologia tropical 51, 355-359.

Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. Advances in Marine Biology 40, 81-251.

Kathiresan, K., Rajendran, N., 2005. Coastal mangrove forests mitigated tsunami. Estuarine Coastal and Shelf Science 65, 601-606.

Khan, N.A., Nazar, R., Iqbal, N., Anjum, N.A. (Eds.), 2012. Phytohormones and abiotic stress tolerance in plants. Springer-Verlag Berlin Heidelberg.

Kilifi District Planning Team, 2000. Kilifi District long-term strategic development plan 2001 - 2015. Kilifi District Development Programme (KDDP).

Kimeli, A.K., 2013. Sedimentation in response to sea level rise in mangroves of Mwache creek, Mombasa-Kenya: a field and modelling study. In, Oceans and Lakes. Vrije Universiteit Brussels, Universiteit Antwerpen and Universiteit Gent, Brussels.

Kirui, K.B., Kairo, J.G., Bosire, J., Viergever, K.M., Rudra, S., Huxham, M., Briers, R.A., 2012. Mapping of mangrove forest and cover change along the Kenya coastline using Landsat imagery. Ocean & Coastal Management, 1-6.

Kitheka, J.U., 1997. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. Estuarine, Coastal and Shelf Science 45, 177-187.

Kitheka, J.U., Ongwenyi, G.S., Mavuti, K.M., 2002. Dynamics of suspended sediment exchange and transport in a degraded mangrove creek in Kenya. Ambio 31, 580-587.

Kitheka, J.U., Ongwenyi, G.S., Mavuti, K.M., 2003. Fluxes and exchange of suspended sediment in tidal inlets draining a degraded mangrove forest in Kenya. Estuarine Coastal and Shelf Science 56, 655-667.

Koedam, N., Dahdouh-Guebas, F., 2009. Ecological quality changes precede changes in quantity in mangrove forests. Science Magazine: Published E-Letter responses to Barbier *et al*., 2008; Science 319: 321-323., 6-8.

Kokwaro, J.O., 1985. The distribution and economic importance of the mangrove forests of Kenya. Journal of East African Natural History Society 75, 1-12.

Konrad, W., Roth-Nebelsick, A., 2003. The dynamics of gas bubbles in conduits of vascular plants and implications for embolism repair. Journal of Theoretical Biology 224, 43-61.

Kovacs, J., 2000. Perceptions of environmental change in a tropical coastal wetland. Land Degradation & Development 11, 209-220.

Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiology Monograph No. 1.

Kramer, P.J., Boyer, J.S., 1995. Water relations of plants and soils. Academic Press, San Diego, California.

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.

Kridiborworn, P., Chidthaisong, A., Yuttitham, M., Tripetchkul, S., 2012. Carbon sequestration by mangrove forest planted specifically for charcoal production in Yeesarn, Samut Songkram. Journal of Sustainable Energy & Environment 3, 87-92.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: A review. Aquatic Botany 89, 201-219.

Kumara, M.P., Jayatissa, L.P., Krauss, K.W., Phillips, D.H., Huxham, M., 2010. High mangrove density enhances surface accretion, surface elevation change, and tree survival in coastal areas susceptible to sea-level rise. Oecologia 164, 545-553.

Kumpf, R.P., Nowack, M.K., 2015. The root cap: a short story of life and death. Journal of Experimental Botany.

Lacerda, L.D., Conde, J.E., Kjerfve, B., 2002. American mangroves. In: Larceda, L.D. (Ed.), Mangrove ecosystems: Function and Management. Springer, Berlin, Germany, pp. 1-62.

Ladjal M, Huc R, Ducrey M (2005) Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. Tree Physiology 25, 1109-1117.

Lambers, H., Stuart Chapin III, F., Pons, T.L., 1998. Plant physiological ecology. Springer New York, Inc, New York, USA.

Larcombe, P., Ridd, P.V., 1996. Dry season hydrodynamics and sediment transport in mangrove creeks. In: Pattariatchi, C. (Ed.), Mixing processes in estuaries and coastal seas. American Geophysical Union, Washington, DC, pp. 388-404.

Laur, J., Hacke, U.G., 2014. The Role of Water Channel Proteins in Facilitating Recovery of Leaf Hydraulic Conductance from Water Stress in Populus trichocarpa. PLoS ONE 9(11): e111751. doi:10.1371/journal.pone.0111751.

Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. Global Ecol. Biogeogr. 23, 726-743.

Lens, F., Tixier, A., Cochard, H., Sperry, J.S., Jansen, S., Herbette, S., 2013. Embolism resistance as a key mechanism to understand adaptive plant strategies. Current Opinon in Plant Biology 16, 287-292.

Lens, F., Sperry, J.S., Christman, M.A., Choat, B., Rabaey, D., Jansen, S., 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. New Phytologist 190, 709-723.

Lewis, A.M., 1992. Measuring the hydraulic diameter of a pore or conduit. American Journal of Botany 79, 1158-1161.

Lieth, H., Berlekamp, J., Fuest, S., Riediger, S., 1999. CD 1 - Climate Diagram World Atlas. Backhuys Publishers, Leiden.

Loepfe, L., Martinez-Vilalta, J., Piñol, J., Mencuccini, M., 2007. The relevance of xylem network structure for plant hydraulic efficiency and safety. Journal of Theoretical Biology 247, 788-803.

Longstreth, D.J., Nobel, P.S., 1979. Salinity effects on leaf anatomy. Plant Physiology 63, 700-703.

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

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

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

Lovelock, C.E., Ball, M.C., Feller, I.C., Engelbrecht, B.M.J., Ewe, M.L., 2006c. Variation in hydraulic conductivity of mangroves: influence of species, salinity, and nitrogen and phosphorous availability. Pysiologia Plantarum 127, 457-464.

Lovelock, C.E., Ball, M.C., Martin, K.C., Feller, I.C., 2009. Nutrient enrichment increases mortality of mangroves. PLoS One 4, e5600.

Lovelock, C.E., Feller, I.C., Adame, M.F., Reef, R., Penrose, H.M., Wei, L.L., Ball, M.C., 2011. Intense storms and the delivery of materials that relieve nutrient limitations in mangroves of an arid zone estuary. Functional Plant Biology 38, 514-522.

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

Lovelock, C.E., Feller, I.C., McKee, K.L., Engelbrecht, B.M.J., Ball, M.C., 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panamá. Functional Ecology 18, 25-33.

Lovelock, C.E., Sorrell, B.K., Hancock, N., Hua, Q., Swales, A., 2010. Mangrove forest and soil development on a rapidly accreting shore in New Zealand. Ecosystems 13, 437-451.

Machăĉkovă, I., Romanov, G.A., 2002. Phytohormones in plant biotechnology and agriculture. In, Proceedings of the NATO-Russia Workshop, Moscow.

Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the indo-west-pacific region. Advances in Marine Biology 6, 73-270.

Maherali, H., Pockman, W.T., Jackson, R.B., 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85, 2184-2199.

Mangala, S., Padma, S., 1998. Status, diversity and conservation of the mangrove forests of Sri Lanka. . J. South Asian nat. Hist. 3, 79-102.

Manzoni, S., Vico, G., Katul, G., Palmroth, S., Jackson, R.B., Porporato, A., 2013. Hydraulic limits on maximum plant transpiration and the emergence of the safety-efficiency trade-off. New Phytol. 198, 169-178.

Marchand, C., Baltzer, F., Lallier-Vergés, E., Albéric, P., 2004. Pore-water chemistry in mangrove sediments in relationship to species composition and developmental stage (French Guiana). Marine Geology 208, 361-381.

Marchand, C., Lallier-Vergés, E., Allenbach, M., 2011. Redox conditions and heavy metals distribution in mangrove forests receiving shrimp farm effluents (Teremba bay, New Caledonia). Journal of Soils and Sediments 11, 529-541.

Marciszewska, K., Tulik, M., 2013. Hydraulic efficiency and safety of xylem sap flow in relation to water stress in woody plants. Intech http://dx.doi.org/10.5772/56656.

Marcus, R.R., 2001. Seeing the forest for the trees: integrated with conservation and development projects and local perceptions of conservation in Madagascar. Human Ecology 29.

Mariona, L., Griciara, J., Ovena, P., 2007. wood formation in urban Norway maple trees studied by the micro-coring method. In, Biotechnical faculty, Department of wood science and technology. University of Ljubljana, Slovenia.

Martínez -Vilalta, J., Mencuccini, M., Alvarez, X., Camacho, J., Loepfe, L., Pinol, J., 2012. Spatial distribution and packing of xylem conduits. American Journal of Botany 99, 1-8.

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.

McClanahan, T.R., Mwaguni, S., Muthiga, N.A., 2005. Management of the Kenyan coast. Ocean & Coastal Management.

McCulloh, K.A., Sperry, J.S., 2005. Patterns in hydraulic architecture and their implications for transport efficiency. Tree Physiology 25, 257-267.

McDowell, N., Fisher, R.A., Xu, C.G., Domec, J.C., Holtta, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytol. 200, 304-321.

McDowell, N., Pockman, W.T., Allen, C., Breshears, D.D., Cobb, N., Kolb, T., Sperry, J.S., West, A., Williams, D., Yepez, E., 2008. Mechanisms of plant survival and plant mortality during drought: why do some plants survive while others succumb to drought? The New Phytologist 178, 719-739.

McDowell, N.G., 2011. Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality. Plant Physiology 155, 1051-1059.

McGranahan, G., Balk, D., Anderson, B., 2007. The rising tide: assessing the risks of climate change and human settlements in low elevation coastal zones. Environment and Urbanization 19, 17-37.

Mckee, K.L., 1995. Seedling Recruitment Patterns in a Belizean Mangrove Forest - Effects of Establishment Ability and Physicochemical Factors. Oecologia 101, 448-460.

McKee, K.L., 2011. Biophysical controls on vertical accretion and elevation change in Caribbean mangrove ecosystems. Estuarine Coastal and Shelf Science 91, 475-483.

McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to sea level through biotic controls on change in soil elevation. Global Ecology & Biogeography 16, 545-556.

Meepol, W., 2010. Carbon sequestration of mangrove forests at Ranong biosphere reserve. Journal of Sustainable Energy & Environment 4, 29-44.

Meinzer, F.C., Clearwater, M.J., Goldstein, G., 2001. Water transport in trees: current perspectives, new insights and some controversies. Environ Exp Bot 45, 239-262.

Meinzer, F.C., Grantz, D.A., 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. Plant Cell and Environment 13, 383-388.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009a. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Functional Ecology 23, 922-930.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009b. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Functional Ecology 23, 922-930.

Mencuccini, M., 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant Cell and Environment 26, 163-182.

Meryer, H.A., 1952. Structure, growth, and drain in uneven-aged forests. Journal of Forestry 41, 126-132.

Metcalfe, C.R., Chalk, L., 1957. Anatomy of the dicotyledons; leaves, stem, and wood in relation to taxonomy, with notes on economic uses. Clarendon Press, Oxford.

Mielke, M.S., Matos, E.M., Couto, V.B., de Almeida, A.F., Gomes, F.P., Oliveira, M.P.A., 2005. Some photosynthetic and growth responses of *Annona glabra* L. seedlings to soil flooding. Acta Botanica Brasilica 19, 905-911.

Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: wetlands and water: Report s*ynthesis*. World Resource Institute, Washington DC.

Mirera, D.O., Mtile, A., 2009. A preliminary study on the response of mangrove mud crab (*Scylla serrata*) to different feed types under cage culture. Journal of Ecology & Natural Environment 1, 007-014.

Mohamed, M.O.S., 2008. Are peri-urban mangrove forests viable? Effects of sewage pollution and wood exploitation on the structure and development of the mangroves of Mombasa (Kenya). In, Laboratory of plant science and nature management. Vrije Universiteit Brussel Brussel, p. 181.

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.

Morisita, 1959. Measuring of the dispersion of individuals and analysis of the distribution patterns. . Research Series E Biology 2, 215-235.

M'rabu, E.J., Robert, E.M.R., Lehmann, I., Kioko, E., Dahdouh-Guebas, F., Koedam, N., Unpublished data. Strategies employed by two woodborer species to infest *Sonneratia alba* (J. Smith) in Kenya.

M'rabu, E.J., 2009. The impact of indirect effects of climate change on mangrove associated biodiversity. MSc Thesis. Vrije Universiteit Brussels, Belgium. 64 pp.

Mueller-Dombois, D., Ellenberg, H., 1974. Aims and methods of vegetation ecology. Willey and Sons Inc., New York, U.S.A.

Mukherjee, N., Bill, S., Nabiul, K., Uta, B., Schmitz, N., Dahdouh-Guebas, F., Koedam, N., 2014. Using expert knowledge and modelling to define mangrove composition, functioning and threats and estimate time-frame for recovery. Ecology and Evolution doi: 10.1002/ece3.1085.

Mulkey, S.S., Wright, S.J., Smith, A.P., 1991. Drought acclimation of an understory shrub in a tropical forest American Journal of Botany 78, 579-587.

Mulkey, S.S., Wright, S.J., Smith, A.P., 1993. Comparative physiology and demography of three neotropical forest shrubs: Alternative shade adapted character syndromes. Oecologia 46, 526-537.

Mutua, A.K., Mavuti, K.M., Daro, N., Tackx, M., 2004. Spatial distribution of suspended particulate matter in Mtwapa Creek and Funzi Bay, Kenya. Western Indian Ocean J. Mar. Sci 3, 29-36.

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.

Nardini, A., Lo Gullo, M.A., Salleo, S., 2011. Refilling embolized xylem conduits: Is it a matter of phloem unloading? Plant Science 180, 604-611.

Naylor, R., Drew, M., 1998. Valuing mangrove resources in Kosrae, Micronesia. Environment and Development Economics, pp 471-490.

Nazarea, V., Rhodes, R., Bontoyan, E., Gabriela, F., 1998. Defining indicators which make sense to local people: intra-cultura l variation in perceptions of natural resources. Human Organization 57, 159-170.

Nazim, K., Ahmed, M., Shaukat, S.S., Khan, M.U., Ali, M.Q., 2013. Age and growth rate estimation of grey mangrove *Avicennia marina* (Forsk.) Vierh from Pakistan. Pakistan Journal of Botany 45, 535-542.

Ngware, M.W., Onsomu, E.N., Muthaka, D.I., Manda, D.K., 2006. Improving access to secondary education in Kenya: What can we do? Equal Opportunities International 25, 523-543.

Nicoll, B.C., Ray, D., 1995. Adaptive growth of tree root systems in response to wind action and site conditions. Tree Physiology 16, 891-898.

Niu, J.Y., Gan, Y.T., Zhang, T.W., Yomg, Q.F., 1998. Postanthesis dry matter accumulation and redistribution in spring wheat mulched with plastic film. Crop Science 6, 1562-1568

Ochieng, C., Erftemeijer, P.L.A., 2002. Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh. in Gazi Bay, Kenya. Trees 16, 167-171.

Ogasa, M., Miki, N.H., Murakami, Y., Yoshikawa, K., 2013. Recovery performance in xylem hydraulic conductivity is correlated with cavitation resistance for temperate deciduous tree species. Tree Physisology 33, 335-344

Okello, J.A., 2008. Wood formation in six Kenyan mangrove tree species: relationship with the environment and dendrochronological potential. In, Ecological Marine Management. Vrije Universiteit Brussel and Universiteit Antwerpen, Brussels, p. 58.

Okello, J.A., Kairo, J.G., Okuku, E.O., 2012. Challenging poverty in a healthy environment: a case of the local communities living along Mtwapa Creek, Kenya. In: Yukio, K., Khudori, D. (Eds.), Towards a sustainable ecology: global challenges and local responses in Africa and Asia. UB Press, Western Matang, Indonesia, pp. 21-28.

Okello, J.A., Robert, E.M.R., Beeckman, H., Kairo, J.G., Dahdouh-Guebas, F., Koedam, N., 2014. Effects of experimental sedimentation on the phenological dynamics and leaf traits of replanted mangroves at Gazi Bay. Ecology and Evolution 4, 3187-3200.

Okello, J.A., Schmitz, N., Kairo, J.G., Beeckman, H., Dahdouh-Guebas, F., Koedam, N., 2013. Self-sustenance potential of peri-urban mangroves: a case of Mtwapa Creek Kenya. Journal of Environmental Science & Water Resources 2.

Ong, J.E., Gong, W.K., 2013. Structure, function and management of mangrove ecosystems. ISME mangrove educational book series No. 2 International Society for Mangrove Ecosystems (ISME), Okinawa, Japan, and International Tropical Timber Organization (ITTO), Yokohama, Japan.

Panayotou, T., 1993. The environment in Southeast Asia: problems and policies. Environmental Science and Technology 27, 2270-2274.

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.

Pfeifer, M., Burgess, N.D., Swetnam, R.D., Platts, P.J., Willcock, S., Marchant, R., 2012. Protected areas: Mixed success in conserving East Africa's evergreen forests. PLoS One 7, 1-10.

Pi, N., Tam, N.F.Y., Wu, Y., Wong, M.H., 2009. Root anatomy and spatial pattern of radial oxygen loss of eight true mangrove species. Aquatic Botany 90, 222-230.

Plomion, C., Leprovost, G., Stokes, A., 2001. Wood formation in trees. Plant Physiology 127, 1513-1523.

Pockman, W.T., Sperry, J.S., 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. American journal of botany 87, 1287-1299.

Polidoro, B.A., Carpenter, K.E., Collins, L., Duke, N.C., Ellison, A.M., Ellison, J.C., Farnsworth, E.J., Fernando, E.S., Kathiresan, K., Koedam, N.E., Livingstone, S.R., Miyagi, T., Moore, G.E., Nam, V.N., Ong, J.E., Primavera, J.H., Salmo III, S.G., Sanciangco, J.C., Sukardjo, S., Wang, Y., Yong, J.W.H., 2010. The loss of species: mangrove extinction risk and geographic areas of global concern. PLoS One 5, 10095.

Pollnac, R.B., Crawford, B.R., 2000. Assessing behavioral aspects of coastal resource use. Proyek Pesir Publications Special Report. Coastal Resource Management Report # 2226. Coastal Resource Centre, University of Rhode Island, Narragansett, Rhode Island., 139pp.

Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: a quantitative review. Australian Journal of Plant Physiology 27, 595-607.

Primavera, J.H., 1997. Socio-economic impacts of shrimp culture. Aquaculture Research 28, 815-827.

PUMPSEA, W.-S., 2005. Part I; Determination of sediment characteristics (density, water content and organic content). In, Experimental protocol for PUMPSEA Work Package 1- SDU. Institute of Biology, University of Southern Denmark.

Purnobasuki, H., Suzuki, M., 2005. Functional anatomy of air conducting network on the pneumatophores of a mangrove plant, *Avicennia marina* (Forsk.) Vierh. Asian Journal of Plant Sciences 4, 334-347.

Quisthoudt, K., Adams, J., Rajkaran, A., Dahdouh-Guebas, F., Koedam, N., Randin, C.F., 2013. Disentangling the effects of global climate and regional land-use change on the current and future distribution of mangroves in South Africa. Biodiversity and Conservation 22, 1369-1390.

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

Reich, P., Ellsworth, D., Walters, M., 1998. Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. Functional ecology 12, 948-958.

Republic of Kenya, Draft 2015. National mangrove management plan. State Department of Environment and Natural Resources.

Rist, R.C., Frederic, P.M., Fernadez, A.M. (Eds), 2016. Poverty, Inequality, and Evaluation: Changing Perspectives. Washington, DC: World Bank. doi:10.1596/978-1-4648-0703-9. License: Creative Commons Attribution CC BY 3.0 IGO.

Robert, E.M.R., Koedam, N., Beeckman, H., Schmitz, N., 2009a. 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., 2011. Successive Cambia: A Developmental Oddity or an Adaptive Structure? PLoS ONE 6, e16558.

Robert, E.M.R., Schmitz, N., Kirauni, H.A., Beeckman, H., Koedam, N., 2009b. Salinity fluctuations in mangrove forest of Gazi Bay, Kenya: lessons for future research. Nature & Faune 24, 89-95.

Robert, E.M.R., Schmitz, N., Okello, J.A., Boeren, I., Beeckman, H., Koedam, N., 2010. Mangrove growth rings: fact or fiction? Trees-Structure and Function 25, 49-58.

Roberts, R.W., Ruara, W.W., 1967. Lamu mangroves inventory, part 1 and 2. Spartan Air Services (Canada) and Forest Department.

Robertson, A.I., Phillips, M., 1994. Mangroves as filters of shrimp pond effluent: Predictions and biogeochemical research needs. hydrobiologia 295, 311-321.

Robertson, A.I., Alongi, D.M., 1992. Coastal and estuarine studies: Tropical mangrove ecosystems. American Geophysical Union.

Rochette, P., Belanger, G., Gastonguay, Y., Bootsma, A., Mongrain, D., 2004. Climate change and winter damage to fruit trees in Eastern Canada. Canadian Journal of Plant Science 84, 1113-1125.

Rönnbäck, P., Crona, B., Ingwall, L., 2007. The return of ecosystem goods and services in replanted mangrove forests: perspectives from local communities in Gazi Bay, Kenya. Environmental Conservation 34, 313-324.

Rood, S.B., Patino, S., Coombs, K., Tyree, M.T., 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees-Structure and Function 14, 248-257.

Roth, I., 1981. Structural patterns of tropical barks, Encyclopedia of plant anatomy band IX3. Borntraeger, ISBN 978-3-443-14012-0, Berlin, Germany

Rowland, L., da Costa, A.C.L., Galbraith, D.R., Oliveira, R.S., Binks, O.J., Oliveira, A.A.R., Pullen, A.M., Doughty, C.E., Metcalfe, D.B., Vasconcelos, S.S., Ferreira, L.V., Malhi, Y., Grace, J., M. Mencuccini, M., Meir, P., 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature DOI: 10.1038/nature15539

Ruwa, R.K., 1990. Mangrove wetlands in Kenya. In: Crafter, S.A., Njuguna, S.G., Howard, G.W. (Eds.), The Wetlands of Kenya. IUCN Communications Division, Gland.

Saenger, P., 2002. Mangrove ecology silviculture and conservation. Kluwer, Dordrecht.

Saenger, P., Moverly, J., 1985. Vegetative phenology of mangroves along the Queensland coastline. Proc. Ecol. Soc. Aust. 13, 257-265.

Saifullah, S.M., Elahi, E., 1992. Pneumatophore density and size in mangroves of Karachi, Pakistan. Pakistan Journal of Botany 24, 5-10.

Saifullah, S.M., Gul, S., Rasool, F., 2004. Anomalous aerial roots in grey mangroves of an arid climate lagoon. Pakistan Journal of Botany 36, 463-466.

Salleo, S., 2006. Phloem as a possible major determinant of rapid cavitation reversal in stems of Laurus nobilis (laurel) Functional Plant Biology 33, 1063-1074.

Salleo, S., Lo Gullo, M.A., Trifilò, 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., Trifilò, P., Nardini, A., Lo Gullo, M.A., 2009. Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for embolism repair? Functional Plant Biology 36, 815-825.

Sammi, J.C., 1961. De Liocourts's method, modified. Journal of Forestry 59, 294-295.

Samoilys, M., Pabari, M., Andrew, T., Maina, G.W., Church, J., Momanyi, A., Mibei, B., Monjane, M., Shah, A., Menomussangab, M., Muttad, D., 2015. Resilience of Coastal Systems and Their Human Partners: Ecological and social profile of coastal systems in Kenya, Mozambique and Tanzania. Nairobi, Kenya: IUCN ESARO, WIOMSA, CORDIO and UNEP Nairobi Convention, x + 74pp.

Sang-Hwan, I., Seokho, I., Dae Yaeon, K., Jeong-gyu, K., 2007. Degradation characteristics of waste lubricants under different nutrient condition. J. Hazard. Mater. 143, 65-72.

Sathirathai S, 1995. Economic valuation of mangroves and the role of local communities in the conservation of natural resources: Case Study of Surat Thani, South of Thailand, *EEPSEA Research Report Series*

Spalding, M.D., Kainuma, M., Collins, L., 2010. World atlas of mangroves. Earthscan, 319 pp.

Satoru, W., Kuraishi, K.S., Naoki, S., 1994. Soil salinity and pH in Japanese mangrove forests and growth of cultivated mangrove plants in different soil conditions. Journal of Plant Resources 107, 39-46.

Savidge, R.A., 1988. Auxin and ethylene regulation of diameter growth in trees. Tree Physiology 4, 401-414.

Scheffer, M., Carpenter, S., Foley, J.A., Folkey, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591-596.

Schenk, H.J., Steppe, K., Jansen, S., 2015. Nanobubbles: a new paradigm for air-seeding in xylem. Trends in Plant Science 20, 1360-1385.

Schmitz, N., Jansen, S., Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2007. Comparative anatomy of intervessel pits in two mangrove species growing along a natural salinity gradient in Gazi Bay, Kenya. Annals of Botany 100, 271-281.

Schmitz, N., Robert, E.M.R., Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2008. A patchy growth via successive and simultaneous cambia: key to success of the most widespread mangrove species Avicennia marina? Annals of Botany 101, 49-58.

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.

Scholander, P.F., Bradstreet, E.D., Hammel, H.T., Hemmingsen, E.A., 1966. Sap Concentrations in Halophytes and Some Other Plants. Plant Physiology 41, 529-532.

Scholz, A., Rabaey, D., Stein, A., Cochard, H., Smets, E., Jansen, S., 2013 The evolution and function of vessel and pit characters with respect to cavitation resistance across 10 *Prunus* species. Tree Physiology 33, 684-694.

Scott, D.B., Frail-Gauthier, J., Mudie, P.J., 2014. Coastal wetlands of the world: geology, ecology, distribution and adaptations. Cambridge University Press.

Sekhwela, M.B.M., Yates, D.J., 2007. A phenological study of the dominant acacia tree species in areas with different rainfall regimes in the Kalahari of Botswana. J Arid Environ 70, 1-17.

Shah, A.A., Kasawani, I., Kamaruzaman, J., 2007. Degradation of Indus delta mangroves in Pakistan. International Journal of Geology 1.

Silvertown, J., Franco, M., McConway, K., 1992. A demographic interpretation of Grime's triangle. Functional ecology 6, 130-136.

Smit, B., Stachowiak, M., 1988. Effects of hypoxia and elevated carbon dioxide concentration on water flux through *Populus* roots. Tree Physiology 4, 153-165.

Smith, A.H., Berkes, F., 1993. Community-based use of mangrove resources in St. Lucia Int. J. Environ. Stud. 43, 123-131.

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

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

Smoak, J.M., Breithaupt, J.L., Smith III, T.J., Sanders, C., 2013. Sediment accretion and organic carbon burial relative to sea-level rise. Catena 104, 58-66.

Snedaker, J.G., 1982. Mangrove species zonation: why? In: Sen, D.N., Rapurohit, K.S. (Eds.), Tasks for Vegetation Science. Junk Publishers, The Hague, Netherlands, pp. 111-125.

Snedaker, S.C., Brown, M.S., Lahmann, E.J., Araujo, R.J., 1992. Recovery of a Mixed-Species Mangrove Forest in South-Florida Following Canopy Removal. Journal of Coastal Research 8, 919-925.

Snedaker, S.C., Jimenez, J.A., Brown, M.S., 1981. Anomalous aerial roots in *Avicennia germinas* L. in Florida and Costa Rica. B Mar Sci 31, 467-470.

Snedaker, S.C., Lahmann, E.J., 1988. Mangrove understory absence - a consequence of evolution. Journal of Tropical Ecology 4, 311-314.

Snoussi, M., Kitheka, J., Shaghude, Y., Kane, A., Arthurton, R., Le Tissier, Martin, Virji, H., 2007. Downstream and coastal impacts of damming and water abstraction in Africa. Environ. Management 39, 587-600.

Spalding, M., Blasco, F., Field, C., 1997. World Mangrove Atlas. The International Society for Mangrove Ecosystems, Okinawa.

Spalding, M.D., Kainuma, M., Collins, L., 2010. World atlas of mangroves. Earthscan, pp 319.

Spurgeon, J. P. G., 2002, Socio-economic assessment and economic valuation of Egypt's mangroves. Final Report, FAO, Rome.

Species 2000, ITIS, Catalogue of life, annual checklist 2013: indexing the world's known species.

Sperry, J.S., Hacke, U.G., Wheeler, J.K., 2005. Comparative analysis of end wall resistivity in xylem conduits. Plant, Cell and Environment 28, 456-465.

Sperry, J.S., Pockman, W.T., 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. Plant, Cell and Environment 16, 279-287.

Stafford-Deitsch, J., 1996. Mangrove: the forgotten habitat. Immel Publishing Limited, London, UK.

Stamm, P., Kumar, P.P., 2010. The phytohormone signal network regulating elongation growth during shade avoidance. Journal of Experimental Botany 61, 2889-2903.

Sterba, H., 2004. Equilibrium curves and growth models to deal with forest in transition to uneven-aged structure- application in two sample stands. . Silva Fennica 38, 413-423.

Steudle, E., 1995. Trees under tension. Nature 378, 663-664.

Steudle, E., 2001. The cohesion-tension mechanism and the acquisition of water by plant roots. Annual Review of Plant Physiology and Plant Molecular Biology 52, 847-875.

Tam, N.F.Y., Wong, Y.S., 1994. Nutrient and heavy metal retention in mangrove sediment receiving wastewater. Water Science and Technology 29, 193-200.

Telewiski, F.W., Lynch, A.M., 1991. Measuring growth and development of stems. In: Lassoie, J.P., Hinckley, T.M. (Eds.), Techniques and approaches in forest tree ecophysiology. CRC Press, Boca Raton, pp. 503-555.

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., 2006. Mangroves and sediment dynamics along the coasts of southern Thailand. In. Wageningen University, Wageningen, p. 126.

Thampanya, U., Vermaat, J.E., Sinsakul, S., Panapitukkul, N., 2006. Coastal erosion and mangrove progradation of Southern Thailand. Estuarine Coastal and Shelf Science 68, 75-85.

Thampanya, U., Vermaat, J.E., Terrados, J., 2002. The effect of increasing sediment accretion on the seedlings of three common Thai mangrove species. Aquatic Botany 74, 315-325.

Thrush, S.F., Hewitt, J., Cummings, V.J., Ellis, J., Hatton, J.C., Lohrer, A., Norkko, A., 2004. Muddy waters: elevating sediment input to coastal and estuarine habitats. Frontiers in Ecology and Environment 2, 299-306.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827-852.

Tomlinson, C.B., 1986. The botany of mangroves. Cambridge University Press, New York, USA.

Tomlinson, P.B., 1994. The botany of mangroves. Cambridge University Press, Cambridge.

Tong, P.H.S., Auda, Y., Populus, J., Aizpuru, M., Al Habshi, A., Blasco, F., 2004. Assesment from space of mangrove evolution in the Mekong Deltain relation to extensive shrimp farming. International Journal of Remote Sensing 25, 4795-4812.

Tonneijck, F., Van Wesenbeeck, B., Spalding, M., 2013. How mangroves help in reducing flooding and coastal erosion. Outreach on Climate Change & Sustainable Development.

Tran Thi, V., Thi Xuan, A.T., Nguyen, H.P., Dahdouh-Guebas, F., Koedam, N., 2014. Application of remote sensing and GIS for detection of long-term mangrove shoreline changes in Mui Ca Mau, Vietnam. Biogeosciences 11, 3781-3795.

Trnka, M., Olesen, K., Kersebaum, K., Skjelvag, A.O., Eitzinger, J., Seguin, B., Peltonen-Sainio, P., Rotter, R., Anaiglesias, A., Cloppet, E., 2011. Agroclimatic conditions in Europe under climate change. Global Change Biology 17, 2298-2318.

Tudela, D., Primo-Millo, E., 1992. 1-Aminocyclopropane-1-carboxylic acid transported from roots to shoots promotes leaf abscission in Cleopatra Mandarin (*Citrus reshni* Hort. ex Tan.) seedlings rehydrated after water stress. Plant Physiology 100, 131-137.

Twilley, R.R., Snedaker, S.C., Yáñez-Arancibia, A., Medina, E., 1996. Biodiversity and ecosystem processes in tropical estuaries: perspectives of mangrove ecosystems. In: Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E., Schulze, E.D. (Eds.), Functional roles of biodiversity: a global perspective. John Wiley & Sons Ltd, pp. 327-370.

Tyree, M.T., 1997. The cohesion-tension theory of sap ascent: current controversies. Journal of Experimental Botany 48, 1753-1765.

Tyree, M.T., Zimmermann, M.H., 2002. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Heidelberg.

Tyree, M.T., 2003. Plant hydraulics: the ascent of water. Nature 423, 923.

Tyree, M.T., Cochard, H., Cruiziat, P., Sinclair, B., Ameglio, T., 1993. Drought-induced leaf shedding in wallnut: evidence for vulnerability segmentation. Plant, Cell and Environment 16, 879-882.

Tyree, M.T., Salleo, S., Nardini, A., Lo Gullo, M.A., Mosca, R., 1999. Refilling of embolized vessels in young stems of Laurel. Do we need a new paradigm? Plant Physiology 120, 11-21.

Tyree, M.T., Sperry, J.S., 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from model. Plant Physiology 88, 574-580.

Tyree, M.T., Sperry, J.S., 1989. Vulnerability of xylem to cavitation and embolism. Annual Review of Plant Physiology and Plant Molecular Biology 40, 19-38.

UNEP, 1998. Eastern Africa Atlas of the coastal resources: UNEP Regional Reports and Studies. No. 1 Nairobi, Kenya.

UNEP, 2001. Eastern African Database and Atlas Project (EAF/14). The Eastern African Coastal Resources Atlas: Kenya. United Nations Environmental Program.

UNEP, 2011. Economic analysis of mangrove forests: A case study in Gazi Bay, Kenya. United Nations Environmental Programme DEW/1230/NA, iii+42pp.

UNICEF, 2014. Kenya at a glance. http://www.unicef.org/kenya/overview_4616.html (accesed on 28/07/2015).

UNICEF, 2015. The state of the world's children 2015: country statistical tables.

Urli, M., Porté, A.J., Cochard, H., Guengant, Y., Burlet, R., Delzon, S., 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees.

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.

Valiela, I., Bowen, J.L., York, J.K., 2001. Mangrove forests: one of the world's threatened major tropical environments. BioScience 31, 807-815.

Van der Stocken, T., De Ryck, D.J.R., Balke, T., Bouma, T.J., Dahdouh-Guebas, F., Koedam, N., 2013. The role of wind in hydrochorous mangrove propagule dispersal. Biogeosciences 10, 3635-3647.

Van Nedervelde, F., Cannicci, S., Koedam, N., Bosire, J., Dahdouh-Guebas, F., 2015. What regulates crab predation on mangrove propagules? Acta Oecologia 63.

Vanacker, V., Von Blanckenburg, F., Govers, G., Molina, A., Poesen, J., Deckers, J., 2007. Restoring dense vegetation can slow mountain erosion to near natural benchmark levels. Geology 35, 303-306.

Vanacker, V., Bellin, N., Molina, A., Kubik, P., 2014. Erosion regulation as a function of human disturbances to vegetation cover: a conceptual model. Landscape Ecology 29, 293-309.

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

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.

Vesala, T., Hölttä, T., Perämäki, M., Nikinmaa, E., 2003. Refilling of a hydraulically isolated embolized xylem vessel: model calculations. Annals of Botany 91, 419-428.

Vidoz, M.L., Loreti, E., Mensuali, A., Alpi, A., Perata, P., 2010. Hormonal interplay during adventitious root formation in flooded tomato plants. The Plant Journal 63, 551-562.

Visser, E.J.W., Bögemann, G.M., Blom, C.W.P.M., Voesenek, L.A.C.J., 1996. Ethylene accumulation in waterlogged Rumex plants promotes formation of adventitious roots. Journal of Experimental Botany 47, 403-410.

Visser, M., Both, C., 2005. Shifts in phenology due to global climate change: The need for a yardstick. Proceedings of Royal the Society 272, 2561-2569.

Viswanathan, P.K., 2011. Mangroves and their multifunctionality: An analysis of the impacts of community based mangrove restoration in Gujarat. In, Indian Society for Ecological Economics, Sixth Biannual Conference, Hyderabad, India.

Voesenek, L.A.C.J., Rijinders, J., Peters, A.J.M., Van de Steeg, H.M.V., De Kroon, H., 2004. Plant hormones regulate fast shoot elongation under water: from genes to communities. Ecology 85, 16-27.

Walters, B.B., 2005. Ecological effects of small-scale cutting of Philippine mangrove forests. Forest Ecology and Management 206, 331-348.

Walters, B.B., Rönnbäck, P., Kovacs, J., Crona, B., Hussain, S., Badola, R., Primavera, J.H., Barbier, E.B., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and adaptive management of mangroves: a review. Aquatic Botany 89, 220-236.

Wang'ondu, V.W., 2009. Vegetative phenology of *Rhizophora mucronata* Lamk., *Avicennia marina* (Forsk.) Vierh. and *Sonneratia alba* Sm. in natural and reforested mangrove forests at Gazi Bay, Kenya. In, Microbiology. University of Nairobi, Kenya and Vrije Universiteit Brussels, Belgium.

Wang, J., Ives, N.E., Lechowicz, M.J., 1992. The relation of foliar phenology to xylem embolism in trees. Functional ecology 6, 469-475.

Wang, L., Mu, M., Li, X., Lin, P., Wang, W., 2010. Differentiation between true mangroves and mangrove associates based on leaf traits and salt contents. Plant Ecology, 1-10.

Wang, L.M., Mu, M.R., Li, X.F., Lin, P., Wang, W.Q., 2011. Differentiation between true mangroves and mangrove associates based on leaf traits and salt contents. J Plant Ecol-Uk 4, 292-301.

Wang’ondu, 2010. Phenology of *Avicennia marina* (Forsk.) Vierh. in a Disjunctly-zoned Mangrove Stand in Kenya.

Wass, P. (Ed.), 1995. Kenya's indigenous forests: status management and conservation. . IUCN, Grand, Switzerland, and Cambridge, UK.

Watson, J.G., 1928. Mangrove forests of the Malay Peninsula. Fraser and Neve, Singapore.

Weinig, C., Delph, L.F., 2001. Phenotypic plasticity early in life constrains developmental responses later. Evolution 55, 930-936.

Weng, J.-K., Chapple, C., 2010. The origin and evolution of lignin biosynthesis. New Phytol. 187, 273-285.

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

Westhoff, M., Zimmermann, D., Schneider, H., Wegner, L.H., Gessner, P., Jakob, P., Bamberg, E., Shirley, S., Bentrup, F.W., Zimmermann, U., 2009. Evidence for discontinuous water columns in the xylem conduit of tall birch trees. Plant Biology 11, 307-327.

Wheeler, J.K., Sperry, J.S., Hacke, U.G., Hoang, N., 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. Plant, Cell and Environment 28, 800-812.

White, A.T., Eisma-Osorio, R.L., Green, S.J., 2005. Integrated coastal management and marine protected areas: Complementarity in the Philippines. Ocean & Coastal Management 48, 948-971.

Whitman, G., 1989. Mangroves of the Nothern Territory, Northern Territory botanical Bulletin No. 7. Conservation Commission of the Northern Territory.

Wilkinson, B.H., 2005. Humans as geological agents: A deep-time perspectives. Geology 33, 161-164.

Williamson, L.C., Ribrioux, S.P.C.P., Fitter, A.H., Leyser, H.M.O., 2001. Phosphate availability regulates root system architecture in Arabidopsis. Plant Physiology 126, 875-882.

Wilson, B.J., Lee, W.G., 2000. C-S-R triangle theory: community-level predictions, tests, evaluation of criticisms, and relation to other theories. Oikos 91, 77-96.

Wimmer, R., 2002. Wood anatomical features in tree-rings as indicators of environmental change. Dendrochronologia 20, 21-36.

Wium-Andersen, S., Christensen, B., 1978. Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. Aquatic Botany 5, 383-390.

Wium-Anderson, S., 1981. Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllacaea* Gaertn. Aquatic Botany 10, 371-376.

Wolanski, E., 1995. Transport of sediment in mangrove swamps. Hydrobiologia 295, 31-42.

Wolanski, E., Gibbs, R.J., 1995. Flocculation of suspended sediment in the Fly River estuary, Papua New Guinea. Journal of Coastal Research 11, 754-762.

Wolanski, E., Mazda, Y., Ridd, P., 1992. Tropical mangrove ecosystems. In: Robertson, A.I., Alongi, D.M. (Eds.), Coastal and estuarine studies. American Geophysical Union, Washington, pp. 43-62.

Wolosewick, J.J., 1980. The application of Polyethylene Glycol (PEG) to electron microscopy. Journal of Cell Biology 86, 675-681.

Wolters, H., Jürgens, G., 2009. Survival of flexible: hormonal growth control and adaptation in plant development. Nature Reviews Genetics 10, 305-317.

Wong, M.H., 2004. Wetlands ecosystems in Asia: function and management. Elsevier B.V.

Woodward, I., 2004. Plant Science: tall storeys. Nature 428, 807-808.

WWF, 2006. Climate change impacts on East Africa: a review of the scientific literature. World Wide Fund For nature, Gland, Switzerland.

Xiao, Y., Wang, W., Chen, L., 2010. Stem anatomical variations in seedlings of the mangrove *Bruguiera gymnorrhiza* grown under periodical waterlogging. Flora 205, 499-505.

Xu, L., Huber, H., During, H.J., Dong, M., Anten, N.P.R., 2013. Intraspecific variation of desert shrub species in phenotypic plasticity in response to sand burial. New Phytol. 199, 991-1000.

Yáñez-Espinosa, L., Flores, J., 2011. A review of Sea-Level Rise effect on mangrove forest species: Anatomical and morphological modifications. In: Casalegno, S. (Ed.), Global warming impacts- case studies on ecology, human health, and on urban and natural environments. In Tech China, pp. 254-276.

Yáñez-Espinosa, L., Terrazas, T., Angeles, G., 2008. The effect of prolonged flooding on the bark of mangrove trees. Trees-Structure and Function 22, 77-86.

Yeung, E.C., 1998. A beginner's guide to the study of plant structure. In: Karcher, S.J. (Ed.), Tested studies for laboratory teaching, Volume 19. Proceedings of the 19th Workshop/Conference of Association for Biology Laboratory Education (ABLE), p. 365.

Young, B.M., Harvey, E.L., 1996. A spatial analysis of the relationship between mangrove (*Avicennia marina* var. *australasica*) physiognomy and sediment accretion in Hauraki plains, New Zealand. Estuarine Coastal and Shelf Science 42, 231-246.

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

Zamski, E., Schaffer, A.A., 1996. Photoassimilate distribution in plants and crops: Source-sink relationships. Mercel Dekker, Inc., Madison Avenue, New York.

Zalamea, M., Gonzalez, G., 2008. Leaffall phenology in a subtropical wet forest in Puerto Rico: from species to community patterns. Biotropica 40, 295-304.

Zhou, Q., Robinson, M., Pilesjo, P., 1998. On-the-ground estimation of vegetation cover in Australian rangelands. International Journal of Remote Sensing 19, 1815-1820.

Zimmermann, D., Westhoff, M., Zimmermann, G., Geßner, P., Gessner, A., Wegner, L.H., Rokitta, M., Ache, P., Schneider, H., Vásquez, J.A., Kruck, W., Shirley, S., Jakob, P., Hedrich, R., Bentrup, F.W., Bamberg, E., Zimmermann, U., 2007. Foliar water supply of tall trees: evidence for mucilage-facilitated moisture uptake from the atmosphere and the impact on pressure bomb measurements. Protoplasma 232, 11-34.

Zimmermann, M.H., 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.

Zimmermann, U., Schneider, H., Wegner, L.H., Haase, A., 2004. Tansley review. Water ascent in tall trees: does evolution of land plants rely on a highly metastable state? New Phytologist 162, 575-615.

Zimmermann, U., Wagner, H.J., Heidecker, M., Mimietz, S., Schneider, H., Szimtenings, M., Haase, A., Mitlöhner, R., Kruck, W., Hoffmann, R., König, W., 2001. Implications of mucilage on pressure bomb measurements and water lifting in trees rooting in high-salinity water. Trees 16, 100-111.

Zimmermann, U., Zhu, J.J., Meinzer, F.C., Goldstein, G., Schneider, H., Zimmermann, G., Benkert, R., Thürmer, F., Melcher, P., Webb, D., Haase, A., 1994. High molecular weight organic compounds in the xylem sap of mangroves: Implications for long distance water transport. Botanica Acta 107, 218-229.

Zorini, L.O., Contini, C., Jiddawi, N., Ochiewo, J., SHunula, J., Cannicci, S., 2004. Participatory appraisal for potential community-based mangrove management in East Africa. Wetlands Ecology and Management 12, 87-102.

Zotz, G., Tyree, M.T., Patiño, S., 1997. Hydraulic architecture and water relations of a flood-tolerant tropical tree, Annona glabra. Tree Physiology 17, 359-365.

Appendices:

Appendix I: Additional Information

Table S1 Taxonomic divisions of various mangrove species across the globe, status in the IUCN Red List (LC-least concern, VU-vulnerable, NT- near threatened, EN- endangered, DD- Data deficient)

Family	**Genus**	**Species**	**Subspecies**	**Varriety**	**Authour**	**Category**$^{\psi}$	**IUCN status**
Arecaceae	*Nypa*	*fruticans*			(Thunb.) Wurmb.	***	LC
Acanthaceae	*Avicennia*	*alba*			Blume	***	LC
Acanthaceae	*Avicennia*	*bicolor*			Standley	***	VU
Acanthaceae	*Avicennia*	*germinans*			(L.) Stearn	***	LC
Acanthaceae	*Avicennia*	*integra*			N.C. Duke	***	VU
Acanthaceae	*Avicennia*	*lanata*			Ridley	***	
Acanthaceae	*Avicennia*	*marina*			(Forsk.) Vierh.	***	LC
Acanthaceae	*Avicennia*	*marina*		var. *acutissima*	Stapf & Moldenke ex Moldenke	***	
Acanthaceae	*Avicennia*	*marina*		var. *anomala*	Moldenke	***	
Acanthaceae	*Avicennia*	*marina*		var. *australasica*	(Walp.) Moldenke ex. N.C. Duke	***	
Acanthaceae	*Avicennia*	*marina*		var. *eucalyptifolia*	(Valet.) N.C. Duke	***	
Acanthaceae	*Avicennia*	*marina*		var. *marina*	(Forsk.) Vierh.	***	
Acanthaceae	*Avicennia*	*marina*		var. *resinifera*	(Fort.) Bakhuizen	***	
Acanthaceae	*Avicennia*	*marina*		var. *rumphiana*	(Hall. f.) Bakhuizen	***	
Acanthaceae	*Avicennia*	*officinalis*			L.	***	LC
Acanthaceae	*Avicennia*	*rumphiana*			Hall.f.	***	VU
Acanthaceae	*Avicennia*	*schaueriana*			Stapf and Leechman ex Moldenke	***	LC
Acanthaceae	*Acanthus*	*ebracteatus*			Vahl.	Associate	LC
Acanthaceae	*Acanthus*	*ilicifolius*			L.	Associate	LC
Acanthaceae	*Acanthus*	*volubilis*			Wall.	Associate	LC
Acanthaceae	*Acanthus*	*xiamenensis*			R.T. Zhang	Associate	DD
Malvaceae	*Camptostemon*	*philippinensis*			(Vidal) Becc.	Minor	EN
Malvaceae	*Camptostemon*	*schultzii*			Masters	Minor	LC
Combretaceae	*Conocarpus*	*erectus*			L.	Asc	
Combretaceae	*Laguncularia*	*racemosa*			(L.) Gaertn.f.	***	LC
Combretaceae	*Lumnitzera*	*littorea*			(Jack) Voigt	***	LC
Combretaceae	*Lumnitzera*	*racemosa*			Willd.	***	LC
Combretaceae	*Lumnitzera*	*rosea*			(Gaud.) Presl.	***	LC
Euphorbiaceae	*Excoecaria*	*agallocha*			L.	Minor	LC
Euphorbiaceae	*Excoecaria*	*agallocha*	*agallocha*		L.	Minor	
Euphorbiaceae	*Excoecaria*	*agallocha*	*ovalis*		(Endl.) Mull.Arg.	Minor	
Euphorbiaceae	*Excoecaria*	*indica*			(Willd.) Muell.-Arg.	Minor	
Lecythidaceae	*Barringtonia*	*asiatica*			(L.) Kurz.	Associate	
Lecythidaceae	*Barringtonia*	*conoidea*			Griff.	Associate	
Lecythidaceae	*Barringtonia*	*racemosa*			(L.) Spreng.	Associate	
Lythraceae	*Pemphis*	*acidula*			Forst.	Minor	LC
Meliaceae	*Xylocarpus*	*granatum*			König	Minor	LC
Meliaceae	*Xylocarpus*	*mekongensis*			Pierre	Minor	
Meliaceae	*Xylocarpus*	*moluccensis*			(Lamk.) Roem.	Minor	LC
Primulaceae	*Aegiceras*	*corniculatum*			(L.) Blanco	Minor	LC
Primulaceae	*Aegiceras*	*floridum*			Roemer and Schultes	Minor	NT
Myrtaceae	*Osbornia*	*octodonta*			F. Muell.	Minor	LC
Tetrameristaceae	*Pelliciera*	*rhizophoreae*			Triana and Planchon	Minor	VU
Plumbaginaceae	*Aegialitis*	*annulata*			R. Brown	Minor	LC
Plumbaginaceae	*Aegialitis*	*rotundifolia*			Roxburgh	Minor	NT
Pteridaceae	*Acrostichum*	*aureum*			L.	Associate	LC
Pteridaceae	*Acrostichum*	*danaeifolium*			Langsdorff and Fischer	Associate	LC
Pteridaceae	*Acrostichum*	*speciosum*			Willdenow	Associate	LC
Rhizophoraceae	*Bruguiera*	*cylindrica*			(L.) Blume	***	LC
Rhizophoraceae	*Bruguiera*	*exaristata*			Ding Hou	***	LC
Rhizophoraceae	*Bruguiera*	*gymnorrhiza*			(L.) Lamk.	***	LC
Rhizophoraceae	*Bruguiera*	*hainesii*			C.G. Rogers	***	CR
Rhizophoraceae	*Bruguiera*	*parviflora*			Wight and Arnold ex Griffith	***	LC
Rhizophoraceae	*Bruguiera*	*x rhynchopetala*			(W.C.Ko) X.-J.Ge & N.C.Duke	***	
Rhizophoraceae	*Bruguiera*	*sexangula*			(Lour.) Poir.	***	LC

Table S1. Continued.. Taxonomic divisions of various mangrove species across the globe, status in the IUCN Red List (LC-least concern, VU-vulnerable, NT- near threatened, EN- endangered, DD- Data deficient).

Family	Genus	Species	Sub species	Varriety	Authour	Category$^{\psi}$	IUCN status
Rhizophoraceae	*Ceriops*	*australis*			(C.T.White) Ballment, T.J.Sm. & J.A.Stoddart	***	LC
Rhizophoraceae	*Ceriops*	*decandra*			(Griff.) Ding Hou	***	NT
Rhizophoraceae	*Ceriops*	*somalensis*			Chiov.	***	
Rhizophoraceae	*Ceriops*	*tagal*			(Perr.) C.B. Robinson	***	LC
Rhizophoraceae	*Ceriops*	*zippeliana*			Blume	***	LC
Rhizophoraceae	*Kandelia*	*candel*			(L.) Druce	***	LC
Rhizophoraceae	*Kandelia*	*obovata*			C.-R. Sheue, H.-Y. Liu & J.W.H. Young	***	LC
Rhizophoraceae	*Rhizophora*	*annamalayana*			Kathiresan	***	
Rhizophoraceae	*Rhizophora*	*apiculata*			Bl.	***	LC
Rhizophoraceae	*Rhizophora*	*mangle*			L.	***	LC
Rhizophoraceae	*Rhizophora*	*mucronata*			Lamk.	***	LC
Rhizophoraceae	*Rhizophora*	*racemosa*			Meyer	***	LC
Rhizophoraceae	*Rhizophora*	*samoensis*			(Hochr.) Salvoza	***	NT
Rhizophoraceae	*Rhizophora*	*stylosa*			Griff.	***	LC
Rhizophoraceae	*Rhizophora*	x *harrisonii*			Leechman	***	
Rhizophoraceae	*Rhizophora*	x *lamarckii*			Montr.	***	
Rhizophoraceae	*Rhizophora*	x *neocaledonica*				***	
Rhizophoraceae	*Rhizophora*	x *selala*			(Salvoza) Tomlinson	***	
Rubiaceae	*Scyphiphora*	*hydrophyllacea*			Gaertn.f.	Minor	LC
Lythraceae	*Sonneratia*	*alba*			J. Smith	***	LC
Lythraceae	*Sonneratia*	*apetala*			Buch.-Ham.	***	LC
Lythraceae	*Sonneratia*	*caseolaris*			(L.) Engler	***	LC
Lythraceae	*Sonneratia*	*griffithii*			Kurz	***	CR
Lythraceae	*Sonneratia*	*hainanensis*			W.C. Ko, E.Y.Chen & W.Y.Chen	***	
Lythraceae	*Sonneratia*	*lanceolata*				***	LC
Lythraceae	*Sonneratia*	*ovata*			Backer	***	NT
Lythraceae	*Sonneratia*	x *gulngai*			N.C. Duke	***	
Lythraceae	*Sonneratia*	x *urama*			N.C. Duke	***	
Malvaceae	*Heritiera*	*fomes*			Buch.-Ham.	Minor	EN
Malvaceae	*Heritiera*	*globosa*			Kostermans	Minor	EN
Malvaceae	*Heritiera*	*kanikensis*			N.C. Majumdar & L.K. Banerjee	Minor	
Malvaceae	*Heritiera*	*littoralis*			Dryand.	Minor	LC

*** major mangrove component

Table S2 Extraction of mangrove wood products within Kilifi county between the years 1990 and 2012 (Source, Kenya Forest Services Kilifi county, Kenya).

Year	Harvested (scores)				Other goods and services	Revenue (KSh)	Remarks- estimated illegal extractions	
	Pau	Mazio	Boriti	Vigingi			Poles (scores)	Fuelwood (m^3)
1990	1260			1135		110 437	220	80
1991	4325			1744		199 279	700	72
1992	-			768		57 592	65	169
1993	3690			2763		332 630.70	712	200
1994	4105			1783		267 485	580	230
1995	3579			2785		357 713.50	620	235
1996	2257			30		130 223	100	260
1997	1346			394		133 746.50	153	250
1998	2335			11		184 467	235	350
1999	1002			110		86 976	100	302
2000	-			-		-	98	305
2001	-			-			260	309
2002	-			-		-	579	312
2003	-			-		-	1400	300
2004	-			-		-	768	330
2005	-			-		-	800	327
2006	-			201		61 474	506	310
2007	-			267		81 690	540	345
2008	-			110		66 145	475	360
2009	-			147		88 060	650	315
2010	-			202	307 300.00	428 600	350	326
2011	-			101	844 000.00	904 590	301	346
2012	-			70	1 072 300.00	1 114 360	254	360

Blanks are missing data as KFS could not account for this. Hyphens are zero values

Table S3 Structural attributes (mean tree height, diameter at half height-$D_{1/2ht}$, diameter at 30 cm D_{30cm} and at breast height D_{130cm}) of the three studied mangrove tree species (*Avicennia marina*, *Ceriops tagal*, and *Rhizophora mucronata*) subjected to sediment burial simulating three different levels of sedimentation (15, 30 and 45 cm). The phenological dynamics were observed over a period of one year in each of the species.

Tree species	Treatment (sediment level)	Mean height (m)	Mean diameter (cm)		Number of trees		ɠAerial roots remain exposed	Phenology monitoring period
			$D_{1/2\,ht}$	D_{30cm} / D_{130cm}	total #	candidate		
A. marina	Control	1.16	0.81	1.43	14	4	All	May 2011 -April 2012
	15cm	1.65	0.99	1.95	15	4	10%	
	30cm	1.37	0.88	1.55	11	4	None	
	45cm	1.9	1.21	2.12	15	4	None	
C. tagal (landward)	Control	1.49	6.6	4.93	9	6	All	Jan 2011-Dec 2011
	15cm	1.51	7.93	5.08	6	6	None	
	30cm	1.37	6.74	4.7	6	6	None	
	45cm	1.35	4.16	6.33	10	6	None	
C. tagal (seaward)	Control	1.13	6.41	4.04	8	6	All	
	15cm	1.98	7.25	4.97	10	6	None	
	30cm	2.05	9.21	5.93	6	6	None	
	45cm	2.22	7.68	5.5	8	6	None	
R. mucronata	Control	3.38		11.39	4	4	All	Nov 2011- Oct 2012
	15cm	3.67		15.5	2	2	68%	
	30cm	3.86		12.63	2	2	61%	
	45cm	3.4		11.77	2	2	31%	

ɠ aerial roots of the mangrove trees were completely buried under certain sedimentation treatments

Table S4 Environmental variables (salinity, height above datum, nutrient levels, porosity and bulk density) measured within the experimental plots of the three studied mangrove tree species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata)* subjected to sediment burial simulating three different levels of sedimentation (15, 30 and 45 cm). Nutrient levels, porosity and bulk density were determined following PUMPSEA (2005) as described in Section 4.2.4 of this disertation.

Species	**Treatment**	**Top 15 cm Salinity (‰)**		**Height**	**Nutrient concentration**			**Porosity (%)**		**Bulk density (g/ cm3)**	
		Max	**Min**	**above datum (**	**PO_4^{3-} -P (µg M)**	**NO_3^- -N (µg M)**	**NH_4^+ -N (µg M)**	**Top 15 cm**	**Bottom***	**Top 15 cm**	**Bottom ***
A. marina	Control	52	36	2.45	0.72 (0.90)	2.44 (3.68)	5.94 (10.43)	0.39±0.10		0.00314 ± 0.0002	
	15 cm	53	33	2.61				0.35±0.01	0.37±0.02	0.00302 ± 0.0004	0.00312 ± 0.0002
	30 cm	46	34.5	2.76				0.26±0.06	0.35±0.06	0.003092 ± 0.0001	0.003276 ± 0.0004
	45 cm	54	34	2.89				0.30±0.03	0.39±0.06	0.003089 ± 0.0001	0.003242 ± 0.0002
C. tagal Landward	Control	51	24	2.56	1.79 (1.37)	2.70 (2.77)	5.73 (10.73)	0.42±0.10		0.003065 ± 0.0001	
	15 cm	51	20	2.71				0.31±0.04	0.35±0.04	0.003489 ± 0.0004	0.003306 ± 0.0004
	30 cm	46	10	2.87				0.31±0.02	0.40±0.05	0.003342 ± 0.0004	0.003464 ± 0.0007
	45 cm	46	28	3.01				0.35±0.03	0.40±0.01	0.003562 ± 0.0004	0.003634 ± 0.0005
C. tagal Seaward	Control	50	27	2.48	1.29 (1.37)	2.25 (2.77)	6.33 (10.73)	0.38±0.04		0.002885 ± 0.0001	
	15 cm	50	23	2.62				0.28±0.02	0. 33±0.07	0.003068 ± 0.0002	0.003072 ± 0.0003
	30 cm	47	21	2.76				0.27±0.07	0.37±0.03	0.002576 ± 0.0001	0.003528 ± 0.0007
	45 cm	48	26	2.93				0.31±0.05	0.37±0.06	0.003277 ± 0.0009	0.003649 ± 0.0008
R. mucronata	Control	40	26	3.09	3.02 (10.74)	0.40 (1.15)	9.53 (10.20)	0.66±0.04		0.002071 ± 0.0003	
	15 cm	42	25	3.31				0.36±0.06	0.43±0.12	0.001964 ± 0.0002	0.001834 ± 0.0002
	30 cm	48	26	3.34				0.33±0.08	0.60±0.06	0.003007 ± 0.0001	0.002968 ± 0.0002
	45 cm	52	15	3.52				0.21±0.03	0.57±0.04	0.003204 ± 0.0002	0.002676 ± 0.0003

Based on height above datum, the plots are flooded 45-59 times a month (Watson, 1928).* Terrestrial sediment- mangrove interphase sampled at 15 cm depth

Appendix II Mtwapa aerial photograph

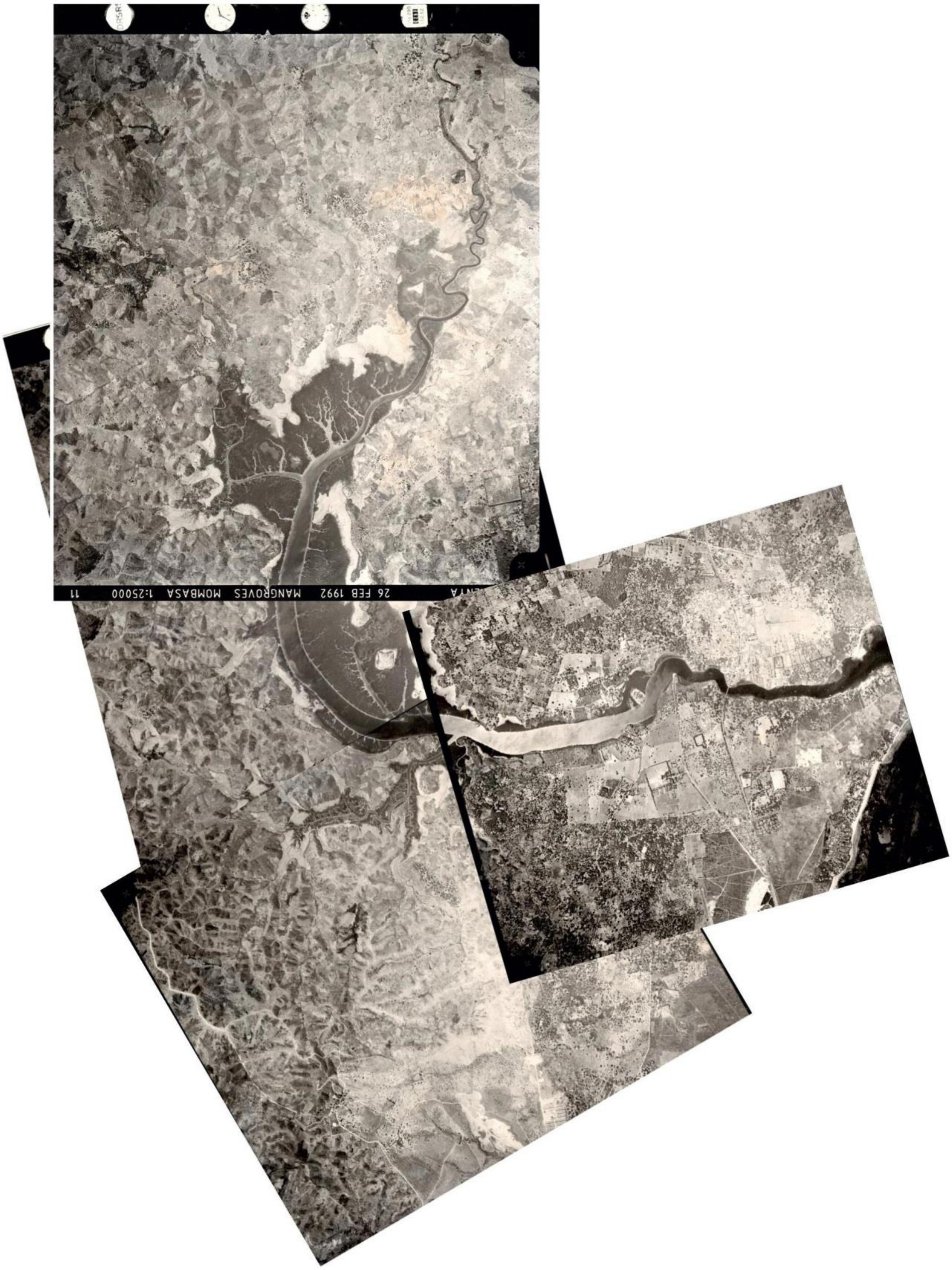


Figure S1: Aerial photographs of Mtwapa Creek used to predetermine location of transects during the structural survey conducted in March 2011. The photographs show mangrove cover as at 29th February 1992 taken at a scale of 1:25000 (source Department of Resource Surveys and Remote sensing, Kenya, DRSRS).

Appendix IIIa Questionnaires

Impacts of human activities on mangrove ecosystem along Mtwapa Creek

Area/village name:__________________ Code:_______ Interview No.:____ Date:_______
Picture No. ____________ GPS Coordinates: __________ °E, ___________ °S

A) Demographic data (tick where applicable)

Marital status: [1]single [2]married [3]divorced [4]widowed [5]separated

Household role: [1]head [2]spouse [3]son/daughter [4]separated

Household size: Number of adults (>18yrs) ______; number of children (< 18yrs) ________

Education level: [ ]none [ ]primary [ ]secondary [ ]tertiary [ ]other, specify________________

Preferred language [ ]Swahili [ ]English [ ]other, specify______________________________

B) Socio-economic information (circle where applicable)

Main occupation: [1]farming [2]fishing [3]casual labor [4]employment [5]trading [6]other__

Income (Ksh/wk): [ ]0-500 [ ]501-1000 [ ]1001-1500 [ ]1500-3000 [ ]>3000

Expenditure: What do you spend most of your money on? [ ]food [ ]shelter [ ]clothing [ ]education [ ]water [ ]other, specify____

House type: [ ]permanent [ ]semi-permanent [ ]temporary

House roof: [ ]makuti [ ]other leaves/bamboo [ ]Iron sheets/tiles [ ]Other__________________

House wall: [ ]makuti leaves [ ]sticks [ ]sticks [ ]mud [ ]stone/bricks [ ]other______________

Cooking fuel: [ ]firewood [ ]charcoal [ ]kerosene [ ]gas [ ]electricity [ ]other_______________

Lighting fuel: [ ]firewood [ ]kerosene [ ]candle [ ]electricity [ ]other

C) Mangrove products

Please give a brief definition of what mangroves are, (categorise answers as):

[ ]no idea [ ]fairly rough [ ]good working knowledge [ ]expert

If respondent has some knowledge continue to (a), if not go to section (D)

(a) Are mangroves harvested in this are? [ ]yes [ ]no. Explain in each case____
____
____

If yes in (a),

(i) Which is the most harvested species? [ ]Mtswi; *A. marina* [ ]mkoko mwembe *B. gymnorhiza* [ ]mkandaa *C. tagal* [ ]mkoko wenyewe *R. mucronata* [ ] Kikandaa *L. racemosa* [ ]Mlilana *S. alba* [ ]Mkomafi *X. granatum*

(ii) Which is the most harvested size? [ ]fito [ ]pau [ ]mazio [ ]boriti [ ]nguzo [ ] vigingi

(iii) Which is the most common mangrove usage? [ ]fuelwood [ ]timber [ ]furniture [ ] medicinal [ ]dye & insecticides [ ]others____________________

(iv) State the major location of harvesting. [ ]nearest to land [ ]nearest to the ocean [ ] heart of the forest [ ]no specific location [ ]other______________

(v) What is the current state of the mangroves in this area? [ ]depleted [ ]recovering [ ]neutral/stable [ ]very healthy

(vi) How do you compare the state to at least 10 years ago? [ ]better [ ]worse [ ]same [ ]no idea

(vii) If worse in (vi) above, which is the major cause? (Otherwise proceed to (ix)) [ ] cutting [ ]sedimentation [ ]climate change [ ]natural hazards [ ]others___________

(viii) Has the state of mangroves affected you in any way? [ ]yes [ ]no

a. If yes, in what major way? [ ]income [ ]health [ ]social activities [ ] environmental [ ]other__________________

b. Give a brief explanation of the impacts stated in viii (a) above:______________

____

____

(ix) Explain what the stae of the forest might be in the future if the current trend continues.____

____

____

D) Land use

i) Main land use: [ ]farming [ ]buiding [ ]leasing [ ]none/idle [ ]other_____________________

If farming or where there is farming:

ii) Which type of farming? [ ]food crop [ ]cash crop [ ]livestock/poultry [ ]fish [ ]agroforestry [ ]other______________________

ii) Which is the major crop grown in the area?____________________________________

iii) How would you describe the amount of rainfall received in the area? [ ]little [ ]sufficient [ ]much [ ]very much

iv) How many farming seasons are there in a year in the area? [ ]numerous [ ]1 [ ]2 [ ]3

v) Please describe the terrain of most of the arable lands here. [ ]steep slopes [ ]gentle slopes [ ] flat [ ]rugged [ ]no idea

vi) Gauge the proximity of the farmland to the creek. [ ]<30 m [ ]31-100 m [ ]101-200 m [ ]201-800 m [ ]>800 m

vii) If steep slopes in (v), which technique of farming is mostly used? [ ]plough along the slope [ ]across the slope [ ]diagonal [ ]other___________________________

viii) What is the major challenge for farmers in the area? [ ]soil infertility [ ]lack of rainfall [ ]lack of seeds [ ]little farming knowledge [ ]insufficient effort [ ]other________________________

ix) If (vii) is soil infertility, probe major cause [ ]erosion [ ]frequent farming [ ]natural [ ]other__________________

Extra for inference

In your opinion, do you think sedimentation can affect mangroves? [ ]yes [ ]no.

Explain your answer____
____

Appendix IIIb Focus group discussion

A sample of focus group discussion question and answers from one of the villages visited (Mtomondoni)

1. What is the main occupation of the residents of this area?

Most of the locals are farmers which is majorly done by men while women have small business enterprices where they sell fast moving household goods such as vegetables, snacks etc., to meet their daily needs. Very few practise fishing around Mtomondoni as most of the fisherfolk come from across the creek in Kidongo and Majaoni villages. While farming has been the major source of income for the locals, most of them are now turning to casual employment due to bad weather and the escalating costs of farm imputs. Men seek employment as casual laborers in building and construction industry and hotels in the nearby quickly expanding Mtwapa town.

2. Are mangrove forests harvested in the area?

Yes mangroves used to be harvested and are still exploited in the area but this has been very minimal. People still depend on the mangroves particularly for building and firewood but access is restricted.

    a. If harvested, what are the major uses?

Mangroves are mainly harvested for building since the poles are strong and termite resistant. Second major use is fuelwood where locals argue that charcoal from mangroves produce more heat energy and burn longer. The harvested poles and fuelwood are either used directly by the exploiters or sold to earn income. Other uses of mangroves which they hear of include habitat and feeding grounds for fish. A few locals therefore understand the ecological importance of mangroves

3. Is harvesting illegal?

Harvesting of mangroves in Mtwapa Creek is illegal and the manning is done by KFS whose guards work to ensure that mangrove poles are not harvested. Building and fencing poles are still however sold secretly while those sold openly in hardwares around Mtwapa town come from Lamu and bare KFS stamp. One would be arrested and arraigned in court if found building with mangrove poles that lack the KFS stamp. However, there are still loopholes in the system as most of the arrested offenders bribe their way out.

4. If not, do you require licence?

Locals are aware that a licence is required for harvesting in other mangrove areas along the coast but Mtwapa mangroves are not open to harvesting. Only permits were issued in the past for collecting firewood of which these is no longer done.

5. How much does it cost for licence, harvesting, transportation and sale?

For collecting firewood (dead wood), one requires a weekly permit that costs Kshs. 40. This is strictly for collecting dry wood and one is not allowed to cut any live standing trees. A bundle of firewood (tita) goes for between KES 100 and KES 150. A smaller bundle with about two to three pieces of wood costs KES 20 to 30. For building poles one requires licences which are anyway not issued for harvesting in Mtwapa Creek.

6. For how long has the local community depended on the mangroves? Has this changed with time in terms of the usage patterns, alternative livelihoods?

For as long as they can remember, mangrove harvesting in Mtwapa has been illegal. The restrictions became even tighter since the year 2000 even minimising further cases of illegal harvesting.

7. How have the communities' livelihood been affected by the change?

Since the ban was tightened, people have had to turn to other sources of building poles which is more expensive. Most of the locals around Mtepeni area depended on mangroves for charcoal burning and selling hence getting money for schooling their children. Some children have had to drop out of school as a result of the ban.

8. How have mangroves changed with time in terms of areal coverage and pole quality?

Mangrove coverage has increased with certain areas close to bare tidal flats getting colonised. However, locals are worried over the pole quality and form of the poles from Mtwapa forest. "We think that mangroves from Mtwapa are different from those in other areas along the Kenyan coast. Probably the species are different". "They have extremely thick barks with crooked thin stems. *Xylocarpus* is quite rare with most *Avicennia* dying out leaving the entire forest almost fully colonised by *Rhizophora*.

9. What exactly can the changes be attributed to?

There has been a ban on harvesting and was even made tighter ten years ago. This restriction has facilitated natural regeneration hence aid in the restoration of the forest. As a result the stem density has increased greatly. Outreach programs have also been initiated by youth organisations such as Abent to encourage conservation and now most people know that mangroves can be planted.

10. In ten /30years how do you foresee the state of the mangrove forest?

-The economy is becoming worse and worse and therefore illegal harvesting will persist. In thirty years, the mangroves will therefore be no more.

-With cutting restricted, the mangrove density is becoming higher and thus in future mangroves will even expand further.

-Human population is increasing at a high rate and the youths do not have jobs hence more idleness. This means there will be even more illegal harvesting and in no time mangroves will disappear. Increasing population also comes with a rise in demand for wood and wood products, thus more and more illegal harvesting.

-With Mtwapa town expanding fast, there will be even greater need for building materials hence more harvesting of mangroves. Mangrove poles are preferred to other terrestrial trees for laying building foundation since they are strong.

11. What do you propose to be done to contain the degradation? (Conservation measures)

There is still a gap existing in sensitisation. People are told not to cut mangroves but no explanation is given. More sensitisation should be done for the local community to understand better. Come up with more and more alternative sources of livelihood in order to check illegal harvesting. Proper security need to be put in place. Advocate for controlled harvesting of mangroves to ensure provision of wood and wood products for the current and future generations.