IMPACTS OF TREE HARVESTING ON THE CARBON BALANCE AND FUNCTIONING IN MANGROVE FORESTS

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DEDICATION

In memory of my father, (the late) Kipkemoi Sigira araap Lasoi. In addition this work is dedicated to my mother, Josephine Taprantich nebo araap Lasoi, who inculcated in me the value of knowledge.

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EXECUTIVE SUMMARY

The importance of mangrove forests to the livelihoods of the local communities as well as to the ecological functioning of coastal ecosystems has been widely recognised. However, mangrove forests are at a high risk of being degraded and lost due to rapid growth of human populations and the economic pressures subjected to the coastal ecosystems. The implications of mangrove deforestation and degradation on the ecological functioning of these systems are far reaching and hence need to be investigated. This study experimentally explored the impacts of small scale cutting of mangroves on the functioning of the ecosystem. Secondly, it aimed to estimate belowground productivity of mangroves, as well as relating aboveground biomass production to belowground root production.

Chapter one gives an over-view of the role of mangroves in carbon sequestration. Particular emphasis is given on the roles of mangroves in climate change mitigation and adaptation, as efficient carbon sinks, coastal stabilization and protection. The controls of carbon fluxes in mangrove forests as well as the impacts of deforestation on mangrove ecosystem functioning are explored. The patterns of mangrove productivity are also discussed.

Chapter two experimentally explores the implications of small scale cutting on carbon fluxes in mangrove forests. The findings indicate that mangrove cutting can enhance additional C emissions of 9.8 ± 7.1 tCO_2 ha^{-1} yr^{-1}. Similarly, small scale cutting can also induce subsidence at the rate of -32 mm yr^{-1} within 2 years of cutting.

Chapter three discusses the impacts of tree canopy removal on the biotic attributes of the mangrove ecosystems. The results show that removal of all vegetation can drastically affect the ability of the forest to rejuvenate. Furthermore, canopy removal significantly influences species composition of macrofaunal communities, whereby, gap-preferring species would colonize and dominate open areas created by canopy removal.

Chapter four gives an insight on the patterns of mangrove forest productivity on a local scale. The findings indicate that even at a local level variation in forest productivity exists, probably due to micro topographic differences and soil factors. The results also confirm the high investment in belowground components. There also exist a possibility of significant relationship between above- and belowground biomass productivity. It is also shown that below-to-aboveground productivity ratios follow similar patterns to below-to-aboveground biomass ratios.

Chapter five provides general conclusions of the preceding chapters putting the findings in line with the current trends in mangrove forest decline. The strategies of reversing mangrove decline are also suggested, including the financial initiatives such as Payment for Ecosystem Services (PES) schemes through strategies such as Reducing Emissions for Deforestation Degradation (REDD+). Finally, a number of recommendations are given including sound management options and further issues arising from this study.

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ABSTRACT

Mangrove forests are considered one of the most efficient natural carbon sinks and their preservation is thus important in climate change mitigation. However, they are declining at higher rates than terrestrial forests, due to human activities; with Kenyan mangroves being no of exception. One of the main drivers of mangrove decline in Kenya is over-exploitation for wood products. The present study aimed to assess (a) the effects of tree removal on the fluxes of greenhouse gases, surface elevation and other ecosystem functions of mangrove forests and (b) mangrove root production. To explore these objectives two experiments were established in the mangrove forests at Gazi bay, Kenya: (i) tree harvest and (ii) mangrove productivity studies. For the tree harvest experiment, ten 12 m x 12 m plots were established in March 2009 in a *Rhizophora mucronata* (Lam.) forest. Five plots were randomly selected and all trees within them were girdled in November 2009 and then cut in May 2010. Gas fluxes of CO_2 and CH_4 were sampled using the chamber technique at monthly intervals from June 2009 to April 2011. Surface elevation dynamics were observed using surface elevation stations (SES). Other variables measured included, macrofaunal abundance and diversity and natural regeneration patterns. For the root productivity experiment, twenty eight 10 m x 10 m plots were established in four mangrove forest types; with each type comprising of *Avicennia marina* (Forsk) Vierh., *Ceriops tagal* (Perr) C. B. Robinson, *R. mucronata* and *Sonneratia alba* (Sm) forests. Ten of the plots were established in *A. marina* and *R. mucronata* forests in Makongeni; while 18 plots comprising all the four species were established at Gazi; six plots each for *A. marina* and *R. mucronata* and three plots each for *C. tagal* and *S. alba* forests. Root production was estimated using the root in-growth technique (two in-growth trenches per plot), while the aboveground

productivity was estimated from measurements of girth increment. Girth increment was measured using dendrometers installed on selected trees, one per plot, in combination with periodic girth measurements of 10 trees per plot. Environmental variables such as height above datum, salinity, grain size and redox potential were measured at the beginning of each experiment and during treatment periods for the tree harvest experiment. Treatment significantly elevated carbon emissions from the mangrove sediments by 14.2 ± 10.3 tCO_2 ha^{-1} (rate of 9.8 ± 7.1 tCO_2 ha^{-1} yr^{-1}) within two years. Similarly, treatment significantly induced subsidence of -51.3 ± 24.3 mm (at a rate of -32.1 ± 8.4 mm yr^{-1}) compared to 11.1 ± 10.1 mm (at a rate of 4.2 ± 1.4 mm yr^{-1}) in control plots in over 2 years after treatment. Decomposition of labile roots in the treated plots was most likely the driver of high emissions of carbon in the treated plots. Soil compaction due to collapse of aeranchyma tissue in roots might have been responsible for subsidence in cut plots. Natural regeneration was drastically affected by cutting, with treated plots having sparse seedlings 450 days after treatment. Gap-preferring ocypodid crabs colonized and became more abundant than sesarmids (usually found in closed canopy forest) in treated plots.

There was significant variation in mangrove forest productivity between Makongeni and Gazi sites, with the mangroves in the former having higher production than those of the latter. *Rhizophora mucronata* forest at Makongeni had a higher aboveground biomass (AGB) than all other forest types. On the other hand *A. marina* forest at Makongeni had the highest belowground biomass (BGB) production. Differences in microtopographical settings and soil factors might have influence the variation in forest productivity between the two sites and between the forest types.

These results underscore the importance of putting in place management options that ensure maintenance of continuous canopy cover and fast regeneration in mangrove forests under wood extraction. In addition, mangrove areas at the seafront should be protected. These results also support other work showing that mangrove forests often allocate a higher proportion of carbon to belowground roots than other forests. A high investment in belowground carbon helps facilitate surface elevation and peat formation, which not only forms important carbon sinks but may also enable mangroves to keep pace with projected sea level rise. Therefore, mangrove management in Kenya and the Western Indian Ocean region should explore options that consider trade-offs between mangrove utilization and minimizing loss of ecosystem functioning such as coastal stabilization and protection. In addition initiatives such as the payment for ecosystem services (PES) schemes e.g. reducing emissions from deforestation and degradation (REDD+) and should be explored as some of the strategies to reverse the declining trend in mangrove forest cover.

CHAPTER ONE: INTRODUCTION

1.1   Carbon Balance in Forest Ecosystems

Terrestrial vegetation forms one of the four major reservoirs of carbon (Houghton, 2007), with forests account for ~ 75 % of carbon stored in terrestrial ecosystems (~ 50 % when carbon in the soil is included) and ~ 40 % of the carbon exchanged annually between the terrestrial biosphere and the atmosphere (Schlesinger, 1997; Houghton, 2005). The net carbon budget of forests is a delicate balance between processes of carbon acquisition and release (Malhi *et al.*, 1999; Valentini *et al.*, 2000; Houghton, 2007). These processes are influenced by climatic and environmental variables and the frequency of disturbance (Malhi *et al.*, 1999). Therefore, forest ecosystems play a significant role in regulating atmospheric CO_2 concentration (Dixon *et al.*, 1994) and hence help to mitigate climate change (Luyssaert *et al.*, 2007).

However, human activities have led to increased CO_2 concentration in the atmosphere with associated effects on climate change (Hamilton *et al.*, 2002). Deforestation and forest degradation are considered a major source of emissions of greenhouse gases (GHGs), contributing 12-20 % of annual anthropogenic GHGs emissions (Houghton *et al.*, 2000; Gullison *et al.*, 2007; van der Werf *et al.*, 2009). The clearing and degradation of forests does not only lead to release of carbon, but also destroys important carbon sinks with future implications for carbon sequestration in the face of global warming (Gibbs *et al.*, 2007). The accelerated deforestation and forest degradation have led to increased interest in accentuating the potential of forests as carbon sinks as one of the mechanisms to combat the effects of climate change.

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1.2 Carbon Dynamics in Mangrove Ecosystems

Mangrove forests occur in protected intertidal areas in the tropical and subtropical regions of the world between 32° N and 38° S, with temperature being the main limiting factor in latitudinal distribution (Tomlinson, 1986; Duke, 1992). They occur over various geomorphological settings ranging from river-dominated, wave-dominated, river and wave-dominated, tide-dominated, drowned bedrock valleys and carbonate settings (Thom, 1967, 1982). The most productive system is the river-dominated because of allochtonous input of rich sediments from rivers (Lugo and Snedaker, 1974; Twilley, 1995). Mangrove forests are estimated to have occupied 75 % of the tropical and subtropical coastlines (Farnsworth and Ellison, 1997), but due to widespread degradation their coverage has reduced by half, currently standing at ~ 15.2 million ha (FAO, 2007; Spalding *et al.*, 2010).

In the Western Indian Ocean (WIO) region mangroves occur in the east African coastline of South Africa, Mozambique, Tanzania, Kenya and Somalia, and in the WIO islands of Comoros, Madagascar, Mauritius, Mayotte and Seychelles. Overall mangrove coverage in the WIO region is ~ 880,000 ha, the bulk of which occur in Mozambique (44 %), Madagascar (34 %) and Tanzania (14 %) (FAO, 2007). The main threats facing the mangroves in the region include over-exploitation for wood products, conversion for other land uses, sedimentation and pollution (Taylor *et al.*, 2003).

Mangrove forests of Kenya cover ~ 46,000 ha representing a decline of ~ 18 % in 25 years from 54,000 ha in 1980 (Doute *et al.*, 1981; Kirui *et al.*, 2012). They are distributed along the coastline, with Lamu and the Tana River Districts holding ~ 70% of the total mangrove

forest coverage, while less extensive mangrove areas occur in Kilifi, Mida creek, Mtwapa in the north and Mombasa, Gazi and Vanga - Funzi areas in the south.

Mangrove forests are among the most productive and biologically important ecosystems as they provide important and unique ecosystem functions to human society and coastal and marine systems (Ewel *et al.*, 1998a; Lovelock, 2008; Nellemann *et al.*, 2009; Donato *et al.*, 2011; 2012). The ecosystem functions provided by mangroves are broadly categorized as: a) provisioning (e.g. timber, food for fauna, fisheries), b) regulatory (e.g. regulation of climate, coastal and stabilization and protection), c) supporting (habitat and refuge for fauna, nutrient cycling) and d) cultural functions (e.g. recreation, spiritual and other non-material benefits) (MEA, 2005).

The high productivity exhibited by mangroves coupled with the high below-ground carbon allocation implies a high potential for mangroves as carbon sinks (Twilley *et al.*, 1992; Ong, 1993; Bouillon *et al.*, 2008; Kristensen *et al.*, 2008a). Mangrove ecosystems are, therefore, considered to be amongst the most carbon-rich ecosystems in the world, with ~ 1000 Mg C ha^{-1} of which 50-90 % is in the soil (Donato *et al.*, 2011) and hence they are one of the most effective of all natural carbon sinks with a global significance despite their relatively small global area (Nellemann *et al.*, 2009; Trumper *et al.*, 2009). In addition, mangroves account for 11 % of the total input of terrestrial carbon into the oceans (Jennerjahn and Ittekkot, 2002; Dittmar *et al.*, 2006) despite comprising < 1 % of the global forest coverage (Valiela *et al.*, 2001; Spalding *et al.*, 2010; Giri *et al.*, 2011).

Whilst below-ground biomass usually accounts for ~20 % of the total biomass in terrestrial forests (*e.g.* Cairns *et al.*, 1997), it often represents up to 40-60 % of the total biomass in mangroves (Briggs, 1977; Chmura *et al.*, 2003; Comley and McGuiness, 2005; Tamooh *et al.*, 2008) and may even exceed above-ground biomass by a factor of four or more (Saintilan, 1997b). Mangrove efficiency in carbon storage is attributed to the slow decomposition of plant materials (Middleton and McKee, 2001; Huxham *et al.*, 2010b), because of the anoxic conditions in which they grow (Alongi *et al.*, 2004) and the high lignin content in mangrove roots (Gleason and Ewel, 2002). In addition to storing autochthonous material, mangroves also trap allochthonous carbon in sediment from rivers and the sea, which contributes to the carbon buried within these ecosystems, thereby encouraging the formation of long-term C stores as mangrove peat (Golley *et al.*, 1962; Fujimoto *et al.*, 1999; Cahoon *et al.*, 2003; McKee *et al.*, 2007c).

Because of continual vertical accretion, mangrove sediments may not attain C saturation, unlike terrestrial soils; soil carbon accumulation in mangrove sediments may therefore continue even in mature forests (Chmura *et al.*, 2003; McKee *et al.*, 2007a). As well as acting as a carbon sink, peat formation in mangrove ecosystems has the added advantage of contributing to surface elevation, thereby helping mangroves to keep pace with projected sea level rise (Cahoon and Lynch, 1997; McKee and Faulkner, 2000; McKee *et al.*, 2007a). Wetland soils are considered peaty when they comprise of at least 12 % organic carbon content (Andriesse, 1988).

Efforts have been made to model the major carbon exchange pathways in mangrove ecosystems (Alongi, 2009). Based on up-scaling of the existing empirical data, as well as indirect estimates, the global gross primary production (GPP) of mangrove forests is estimated to be 735 TgC y^{-1} (Figure 1.1; Alongi, 2009). More than half of this (58 %) is returned to the atmosphere through canopy respiration. However, this might be an underestimate, since this is only leaf respiration, excluding other components such as stem and root respiration (Alongi and Brinkman, 2011).

The global net primary production (NPP) of mangrove forests is estimated to lie between 218 and 300Tg C yr^{-1}, (Twilley *et al.*, 1992; Bouillon *et al.*, 2008; Alongi, 2009). The most widely used proxy for mangrove NPP is annual litter fall (e.g. Twilley *et al.*, 1992; Jennerjahn and Ittekkot, 2002), however, this underestimates NPP because the contributions of aboveground wood and root production and the dissolved organic carbon (DOC) released through root exudates are not accounted for (Kristensen *et al.*, 2008a). Litter fall and aboveground wood production each contribute ~ 20 % of NPP (Alongi *et al.*, 2005; Kristensen *et al.*, 2008a), while belowground root production makes a substantial contribution of ~ 50 % to the NPP (Saenger, 1982; Twilley *et al.*, 1992; Matsui, 1998; Alongi and Dixon, 2000). However, the contribution of belowground root production is likely to be underestimated because (1) there are limited data available due to technical difficulties in quantifying belowground root production (Komiyama *et al.*, 1987; Saintilan, 1997b; Matsui, 1998; Komiyama *et al.*, 2008; Tamooh *et al.*, 2008), (2) most estimates consider only fine roots and (3) organic carbon root exudates are not included (Bouillon *et al.*, 2008; Kristensen *et al.*, 2008a).

$$423 + 42 + 35 = 500R_T$$
$$(R_c) \quad (R_s) \quad (R_{H_2O})$$

735 (GPP)

309 (NPP)

Wood Production 67

68 Litter

H₂O

Soil

174

Fine Root Production

29 Burial

POC 29

DOC 14
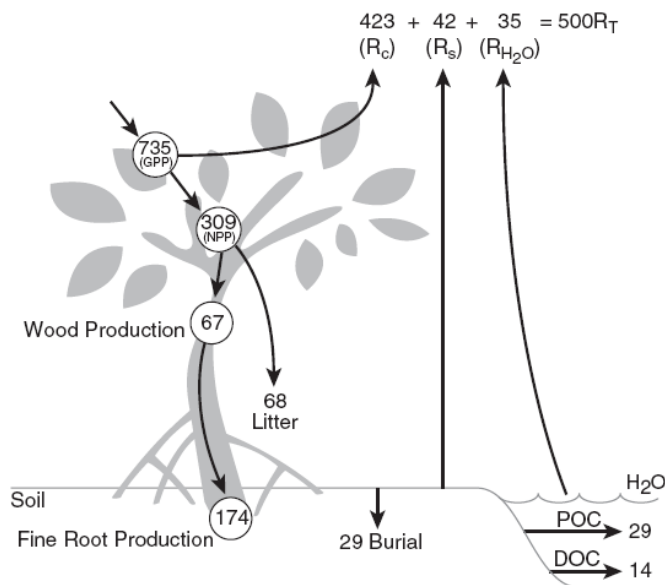
Figure 1.1. Model of the major pathways of carbon flow through the world's mangrove ecosystems: units = TgC year^{-1}. The budget assumes a global mangrove coverage of 16 million ha (Adapted from Alongi; 2009)

The role of mangroves as carbon sources or sinks depends on the balance between mangrove ecosystem productivity and respiration. In determining the carbon balance of mangrove forests the input of carbon by photosynthesis and sediment trapping must be balanced against the losses of carbon through respiration, leaf litter, tidal export to adjacent ecosystems and microbial respiration (Kristensen, 2007; Alongi, 2009). Furthermore, in disturbed systems, anthropogenic factors must also be taken into account (Alongi, 2009). Based on the difference between photosynthetic gains and losses of carbon, mangrove ecosystems are thought to be net autotrophic, with an average net ecosystem production (NEP) of 139 mol C m^{-2} year^{-1} (Alongi, 2009). However, uncertainties exist regarding the fate of carbon fixed by mangrove primary production (Bouillon *et al.*, 2008; Alongi, 2009).

Some of the carbon fixed enters the sediment as plant litter or root exudates which could be eaten by macrofauna, degraded by microbes or buried permanently. Approximately 10 % of NPP is buried in the sediment, while 10-15 % is exported as DOC and POC (Kristensen, 2007). Some of the carbon is returned to the atmosphere via soil respiration (Poungparn *et al.*, 2009), which accounts for ~ 15 % of NPP.

Estimates of soil CO_2 fluxes are usually used as proxies for mineralization, which is likely an underestimate because: firstly, most fluxes are from the surface and subsurface and do not necessarily account for mineralization in deeper soil profiles (Alongi, 2009). Secondly, CO_2 fluxes from the sediment consist of autotrophic and heterotrophic respiration, of which only the latter is due to mineralization.

The CO_2 efflux from the soil accounts for 20-38% of annual input of C to the atmosphere from the terrestrial and marine ecosystems (Raich and Schlesinger, 1992), making it an important determinant of ecosystem C balance and regulator of climate change (Baggs, 2006).The autotrophic and heterotrophic components of soil respiration have been shown to respond differently to environmental changes, thereby altering the net C efflux from soils and the potential for C sequestration. However, separating these two components has been a great challenge to ecological research due to methodological difficulties (Hanson *et al.*, 2000; Epron *et al.*, 2001; Baggs, 2006; Sapronov and Kuzyakov, 2007).

Various techniques that have been employed to separate the components of soil respiration in terrestrial ecosystems include: a) component integration [separate measurements of CO_2 flux from roots, rhizosphere and non-rhizosphere soil] (e.g. Edwards and Harris, 1977), b)

root exclusion (through trenching, root removal, gap formation or tree girdling), (e.g. Hogberg *et al.*, 2001; 2009; Bhupinderpal-Singh *et al.*, 2003; Binkley *et al.*, 2006), c) isotopic techniques (Lin and Ehleringer, 1997; Ekblad *et al.*, 2002) and regression analysis technique (regression of soil CO_2 fluxes against live root biomass) (Kucera and Kirkham, 1971; Rodeghiero and Cescatti, 2006). Each of these techniques has shortcomings as well as suitability to different ecosystems (Baggs, 2006). However, attempts of separating the components of soil respiration by use of any these techniques in mangrove ecosystem have been largely ignored.

The known pathways of C flow (i.e. microbial consumption, burial, soil respiration and export) from mangrove ecosystems only constitute ~ 45 % of the NPP, indicating that there is a significant part of the C budget which is un-accounted for in the system (Bouillon *et al.*, 2008; Alongi, 2009). It has been postulated that this un-accounted C could be dissolved inorganic carbon (DIC) derived from carbon mineralization of organic C, and which is laterally exported by underground water (Bouillon *et al.*, 2008). Alongi (2009) argues that this phenomenon is supported by a number of factors: 1) soil microbes are highly productivity to depths of at least 1 m, 2) lateral drainage of porewater in receding tides has been observed, and 3) the sum of individual carbon metabolism measurements is often greater than the rate of total carbon metabolism measured from the soil surface. Furthermore, measurements of DIC in porewater from mangrove sediments and in waters in channels during tidal ebb have been found to yield similar values (Alongi *et al.*, 2012).

1.3   Controls on Carbon Fluxes from Mangrove Ecosystems

Bacterial decomposition of organic matter in mangrove soils follows a sequence of the availability of electron acceptors. Where oxygen is available, usually at the soil surface and rhizosphere zones, aerobic respiration dominates, but this gives way to suboxic and anoxic pathways of denitrification, manganese, iron and sulphate reduction and methanogenesis. As a result, aerobic respiration and anaerobic sulphate reduction are the major decomposition pathways in mangrove ecosystems (Alongi, 2009). The production of inorganic carbon is due to microbial processes controlled by biological, physical and chemical factors in the soils (Chen *et al.*, 2010). However, the influences of these processes on carbon production in mangrove sediments are complex and as a result, no single factor is an overarching aspect in regulation of microbial decomposition (Alongi, 2009). Nonetheless, microbial activities increase with soil temperature, infaunal and root activities (leachates); hence more CO_2 is produced under these conditions. Similarly, smaller grain size and higher organic matter and nitrogen contents tend to lead to higher CO_2 emissions (Alongi, 2009).

Methane production comprises a small proportion (1-10 %) of microbial decomposition in mangrove soils, hence methanogenic activities have been detected in a few mangrove soils (Alongi *et al.*, 2005; Kristensen, 2007). Methane emissions are generally lower in marine environments than in freshwater systems, because reduction pathways utilising sulphur dominate methanogenic ones when sulphur is available, as it usually is in marine systems (Kristensen, 2007). Methane produced in deeper mangrove sediments, below the depths at which sulphur has been depleted, may be oxidised as it diffuses to the surface. However,

the presence of biogenic structures such as crab burrows, pneumatophores and other belowground roots can serve as conduits through which CH_4 can escape into the atmosphere with minimal risks of oxidation (Andersen and Kristensen, 1988; Kristensen, 2007; Kristensen *et al.*, 2008b). Rates of methanogenesis are also influenced by nutrient enrichment in the soil, salinity, redox potential and to some degree by seasonal changes in soil temperature and soil moisture. Nutrient loading and organic enrichment induces severe oxygen stress and elevates CH_4 emissions (Sotomayor *et al.*, 1994; Purvaja and Ramesh, 2000, 2001). Similarly, freshwater input leading to low salinities and redox potentials tends to decrease sulphate reduction, and thereby stimulates methanogenesis (Sotomayor *et al.*, 1994). Logging may also increase methanogenesis through loss of the oxygen pump in to deeper sediments by roots (Alongi, 2009) and addition of fermentable sugars (Blodau, 2002; Goreau and de Mello, 2007; Kristensen, 2007) from labile debris associated with tree harvesting.

1.4 The Effects of Mangrove Loss on Ecosystem Functioning

Despite their significant roles in global carbon cycling, mangrove forests worldwide are under huge pressure from degradation (Valiela *et al.*, 2001; Alongi, 2002). Though mangrove forests constitute less than 1 % of the global forest cover, they are among the most threatened habitats in the world (Valiela *et al.*, 2001; 2009). Mangrove forests experienced an annual loss of up to 2 % during the 1980 to 2000 period, but declined to 0.7 % per year between 2000 and 2005 (Valiela *et al.*, 2001; FAO, 2007; Giri *et al.*, 2011). The main drivers of mangrove forest loss are aquaculture, wood harvest, and infrastructure and urban development (Abuodha and Kairo, 2001; Valiela *et al.*, 2001; Dahdouh-Guebas *et*

al., 2004). Globally, aquaculture accounts for up to 52 % of mangrove loss, followed by over-exploitation at 26 % (Valiela *et al.*, 2001). However, there are local variations in the main agents of mangrove loss (FAO, 2007; Blanco *et al.*, 2012). Rates of deforestation differ from region to region, with Asia having the highest rates, while south America has the lowest (Table 1.1) (FAO, 2007).

In most areas of the WIO region Mangrove forests are utilized by the local communities for construction and fuelwood (Taylor *et al.*, 2003). In Kenya mangroves are the only natural forests currently licensed by the Kenya Forest Service (KFS) for pole harvesting (Dahdouh-Guebas *et al.*, 2000; Abuodha and Kairo, 2001), albeit without any management system of harvesting. As a result, some mangrove areas are either degraded or completely denuded of vegetation (Bosire *et al.*, 2003; Dahdouh-Guebas *et al.*, 2004). Since mangroves meet ~ 70% of wood requirement of the coastal population (Wass, 1995), there is always a ready market for mangrove poles, especially in major coastal towns.

Licensing procedures involve issuance of permits by KFS to individuals or firms to harvest mangrove poles with a stipulated annual allowable cut for each forest site. The only mangrove forests that are exempted from concession are those within conservation areas (i.e. marine protected areas), all of which are managed by Kenya Wildlife Service (KWS). However, ensuring sustainable harvesting is a daunting task as there are no management plans in place for mangrove exploitation and few resources for policing.

Table 1.1. Current and past mangrove extent by region (1980-2005)

Region	Most recent reliable estimates		1980	1990	Annual change 1980-1990		2000	Annual change 1990-2000		2005	Annual change 2000-2005	
	1000 ha	Ref year	1000 ha	1000 ha	1000 ha	%	1000 ha	1000 ha	%	1000 ha	1000 ha	%
Africa	3,243	1997	3,670	3,428	-24	-0.68	3,218	-21	-0.63	3,160	-12	-0.36
Asia	6,048	2002	7,769	6,741	-103	-1.41	6,163	-58	-0.89	5,858	-61	-1.01
North and Central America	2,358	2000	2,951	2,592	-36	-1.29	2,352	-24	-0.97	2,263	-18	-0.77
Oceania	2,019	2003	2,181	2,090	-9	-0.42	2,012	-8	-0.38	1,972	-8	-0.39
South America	2,038	1992	2,222	2,073	-15	-0.69	1,996	-8	-0.38	1,978	-4	-0.18
World	**15,705**	**2000**	**18,794**	**16,925**	**-187**	**-1.04**	**15,740**	**-119**	**-0.72**	**15,231**	**-102**	**-0.66**

Source: FAO, 2007

Apart from the provision of wood to the local communities, mangrove forests along the Kenyan coast, until 1982, had traditionally provided supply of wood to export markets as far as the Middle East (Abuodha and Kairo, 2001). Over-cutting of mangroves in the past caused serious concerns prompting the government to impose a ban on mangrove cutting for charcoal in 1975. This was followed by a ban on harvesting of mangrove poles for export in 1982, which before then was one of the main causes of depletion of mangrove poles. However, this ban adversely affected the economy of the local communities (Abuodha and Kairo, 2001).

Over-exploitation has seriously reduced the availability of quality poles and has left some areas completely denuded of mangroves (Bosire *et al.*, 2003; Dahdouh-Guebas *et al.*, 2004). Recent analysis of mangrove cover in Kenya indicates that 18 % of forest has been lost between 1985 and 2010, translating to a loss of 0.7 % per year (Kirui *et al.*, 2012). It is projected that the Kenya forest sector is expected to experience a deficit of 6.8 million m^3 wood by the year 2020 (MENR, 1994). Therefore, the pressure on mangrove forests for wood resources is likely to increase due to population pressure and also the fact that mangrove forests are the only natural forests under concession in Kenya.

Anthropogenic activities within and in the proximity of mangrove ecosystems have serious implications on carbon dynamics within the system. Utilization pressures, particularly pole extraction and its consequences are likely to lead to increased emissions of greenhouse gases (GHGs) from mangrove ecosystems to the atmosphere. Considering that ~ 50 % of soil carbon is held within ~ 50 cm of the top layer of the forest soil, continued deforestation

of mangrove forests is projected to release ~112-392 MgC ha^{-1} cleared in to the atmosphere (Donato *et al.*, 2011). This is without accounting for other conversion influences such as decreased carbon sequestration rates and burial efficiency, reduced export to the ocean and the likelihood of increased methanogenesis in disturbed soils.

Apart from carbon losses, mangrove deforestation impacts drastically on other ecological functions of the mangrove ecosystems. The ability of mangroves to keep pace with projected sea-level rise is also likely to be impacted by mangrove forest loss (Gilman *et al.*, 2008). The loss of vegetation implies that surface elevation, which is mediated by vigorous plant growth, is impaired, as is the trapping of sediment by mangrove plants; both these impacts would compromise the future resilience of mangroves (Alongi, 2008; Donato *et al.*, 2011). Loss of trees may not only reduce rates of soil elevation, but may also trigger subsidence or peat collapse, through complex relationships including soil desiccation, consolidation and/or compaction and the collapse of the aerenchyma tissues of plant roots and subsequent root decomposition (Cahoon *et al.*, 2003).

1.5 The Rationale for this Study

Dozens of studies have been published on the emission of GHGs from mangrove ecosystems (e.g. Mukhopadhyay *et al.*, 2002; Lovelock, 2008; Poungparn *et al.*, 2009), however only a few have attempted to study the effects of anthropogenic impacts on the emissions of these gases (e.g. Purvaja and Ramesh, 2001; Kristensen *et al.*, 2008b; Lovelock *et al.*, 2011). Furthermore, the impacted and un-impacted plots used for comparisons are usually located in different sites; hence, there is frequently the possibility

of confounding by other factors such as site conditions or history. Similarly, information on the partitioning of the components of soil respiration; i.e. the autotrophic (root) and heterotrophic respiration, in mangrove ecosystems is very scanty. Although root respiration may contribute significantly to soil respiration, it is difficult to measure separately from that of the soil organic matter decomposition (Goreau and de Mello, 2007). Therefore, there is a need to assess the impacts of human activities, particularly tree removal, on the carbon dynamics and other ecological functioning in mangrove ecosystems. There is also a need to determine the contribution of root respiration to the total soil respiration.

Mangrove deforestation and degradation influence community characteristics within the system. The ecological impacts of deforestation are complex because canopy removal can trigger a chain of events resulting in alteration of environmental conditions and consequently changes in floral and faunal composition (Ewel *et al.*, 1998b; Sherman *et al.*, 2000). Therefore, there is a need to assess the impacts of small-scale disturbance on mangrove forest community dynamics.

Information on mangrove forest productivity is very important in evaluating the carbon balance of the system. Patterns of aboveground productivity of mangrove forests have been widely documented (e.g. Lugo and Snedaker, 1974; Sherman *et al.*, 2003; Komiyama *et al.*, 2008), but few empirical data exist for belowground root productivity (McKee and Faulkner, 2000; Gleason and Ewel, 2002; Cahoon *et al.*, 2003; Sánchez, 2005; Castaneda-Moya *et al.*, 2011). Of the few studies of root productivity, there is hardly any representation of the mangroves of the Western Indian Ocean region.

This study aimed at: a) assessing the impact of mangrove harvesting on carbon cycling and ecosystem functioning, and b) determining rates of belowground production in mangrove forests at Gazi bay, Kenya.

1.6   Objectives

1. To quantify the effects of tree harvesting on:

   a) carbon efflux

   b) root decomposition

   c) sediment accretion and surface elevation dynamics

   d) macrofauna abundance and composition

   e) vegetation recruitment in a mangrove forest at Gazi bay, Kenya.

2. To determine belowground root productivity of the mangrove forests at Gazi bay, Kenya and to explore how this correlates with measures of above-ground productivity
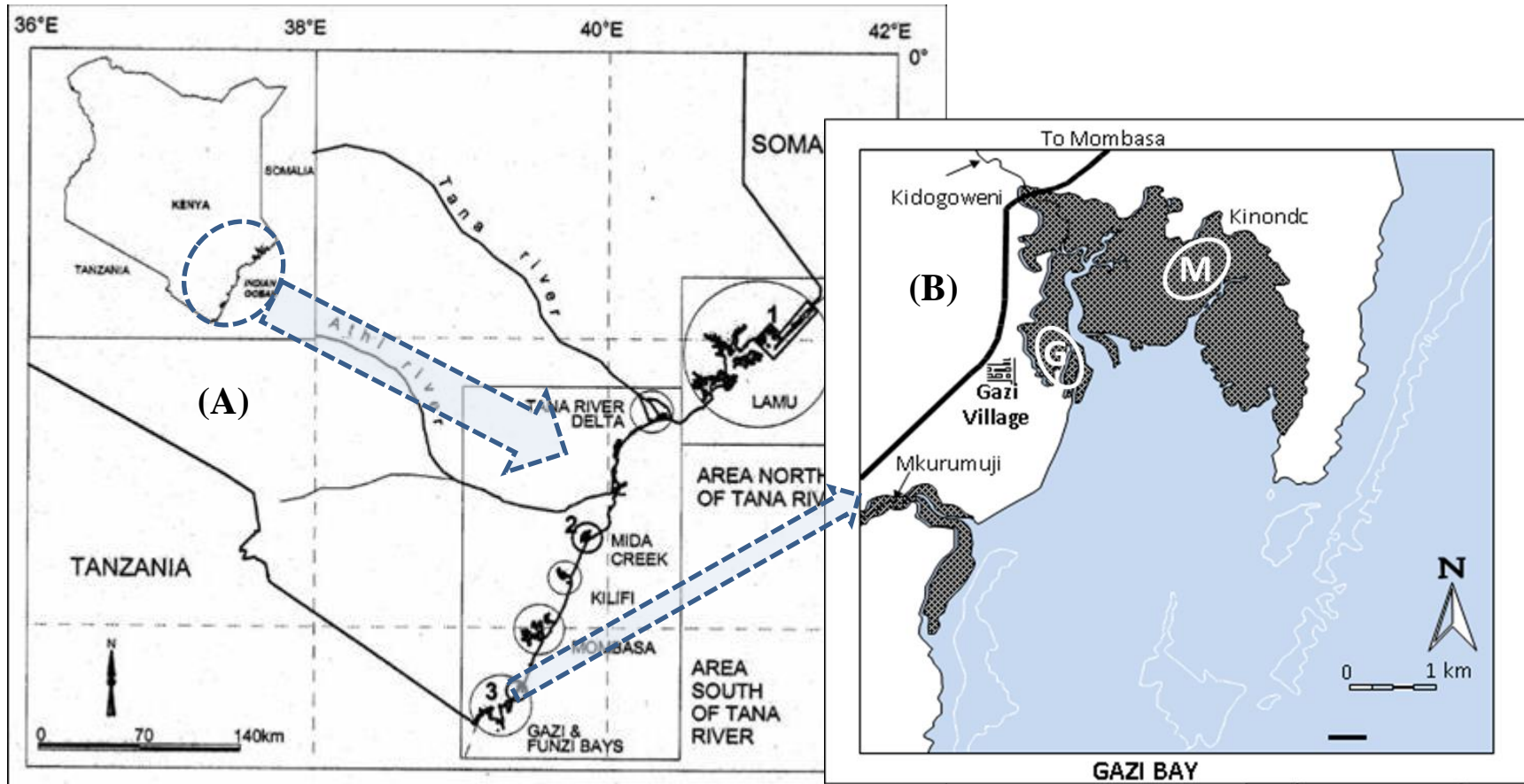
Mangrove forests

Figure 1.2. Map of the Kenyan coast showing (A) mangrove formations along the coastline and (B) the study site, Gazi bay. The top left inset shows the entire map of Kenya, and G and M represent plots established at Gazi and Makongeni mangrove forests, respectively.

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**CHAPTER TWO: THE IMPACTS OF SMALL-SCALE CUTTING ON
CARBON LOSS IN A MANGROVE FOREST AT GAZI BAY, KENYA**

Abstract

Mangroves are amongst the most carbon dense ecosystems. High autochthonous productivity, the trapping of allochthonous materials and slow decomposition in water-logged sediments result in long term storage of substantial carbon stocks below-ground in mangrove forests. The loss of these forests is therefore of global significance for carbon sinks (and also implies the loss of many other ecosystem services). The carbon cycle in mangroves is poorly understood, with around one half of total global production unaccounted for; much of this uncertainty arises from paucity of information on below-ground carbon dynamics. Large scale damage, caused by hurricanes or forest clear felling, can cause rapid carbon losses and enhanced vulnerability to erosion because of subsidence, but it is unclear how this might translate to lower intensity (but more widespread) degradation or wood harvesting. Therefore, this study aimed at quantifying the effects of small scale cutting on the carbon dynamics of mangrove forests. The impact of tree removal on carbon emissions (carbon dioxide, CO_2 and methane, CH_4) from surface sediments, as well as surface elevation dynamics was investigated in a natural mangrove forest at Gazi bay (Kenya). Ten 12 x 12 m plots were established in *Rhizophora mucronata* (Lam.) forest, and five of these were first allocated to girdling treatment (in order to differentiate autotrophic from heterotrophic contributions to sediment respiration), and then followed by cutting after 7 months. The remaining five plots served as the controls. CO_2 and CH_4 fluxes from the sediment were determined by the chamber technique using six chambers per plot. Surface elevation dynamics were determined using surface elevation

stations (SES), with each SES comprising of two 6 mm x 1 m stainless steel rods and marker horizon (MH), randomly installed in each plot. Treatment significantly enhanced carbon emissions within the first year after girdling was initiated, with C emissions in the treated plots exceeding those in the control plots by 1.04 ± 0.43 µmol CO_2 m^{-2} s^{-1} and 5.26 ± 4.20 nmol CH_4 m^{-2} s^{-1}. Similarly, treatment induced a subsidence of -32.1 ± 8.4 mm yr^{-1} over a period of more than 2 years after treatment, while the controls recorded surface elevation of 4.2 ± 1.4 mm yr^{-1}. These results indicate that even small scale tree removal in mangrove forests could contribute significant release of carbon (up to 9.8 ± 7.1 tCO_2 ha^{-1} yr^{-1}). This underscores the threat of human activities to the functioning of mangrove ecosystems and implies that mangrove forest managers need to carefully consider the trade-offs between extracting mangrove timber and losing other mangrove services, particularly carbon storage.

2.1   Introduction

Coastal ecosystems such as mangrove forests, seagrass beds and saltmarshes play important roles in global carbon sequestration (Laffoley and Grimsditch, 2009; Nellemann *et al.*, 2009; McLeod *et al.*, 2011) and hence they are regarded as highly efficient carbon sinks (Donato *et al.*, 2011). Mangrove forests are highly productive systems (Twilley *et al.*, 1992; Bouillon *et al.*, 2008; Kristensen *et al.*, 2008a) and often allocate a large proportion of their energy budget to root production. Because of the presence of aerial root systems, mangroves trap allochthonous organic matter in sediment, with carbon burial rates exceeding those of terrestrial tropical forests by a factor of 50 (Breithaupt *et al.*, 2012).

Unlike terrestrial forest soils, mangrove sediments do not attain C saturation due to continual vertical accretion (McKee *et al.*, 2007a) and hence the sediment C accumulation and the size of C store are likely to continue to increase for a long time (Chmura *et al.*, 2003). Anoxia, low levels of nutrients and the high lignin content of the roots result in slow decomposition of below-ground organic matter (Middleton and McKee, 2001; Gleason and Ewel, 2002; Huxham *et al.*, 2010b) and the accumulation of large reserves of peat and carbon-rich soils (Golley *et al.*, 1962; Fujimoto *et al.*, 1999; Donato *et al.*, 2011). Mangroves are thus amongst the most carbon dense of all forests, often exceeding 900 tonnes C ha^{-1} (Trumper *et al.*, 2009; Donato *et al.*, 2011; Alongi, 2012). In addition, peat formation in mangrove ecosystems contributes to surface elevation, thereby helping mangroves to keep pace with projected sea level rise (Cahoon and Lynch, 1997; McKee and Faulkner, 2000; McKee *et al.*, 2007a).

However, human disturbances (e.g. timber harvesting and clearing) threaten to impair these important environmental processes. Mangrove ecosystems have been altered, degraded or lost at alarming rates; with an estimated 30-50 % of mangroves lost over the past half century (Valiela *et al.*, 2001; 2009). Although rates of loss may be declining (FAO, 2007) they remain high due partly to high poverty levels and dense human populations along tropical coasts (Alongi, 2012). A recent estimate of the total mangrove carbon sink, combined with the known rates of loss, suggested that mangrove destruction can contribute up to 10 % of the annual GHG emissions from land use change (Donato *et al*., 2011).

Therefore, the implications of mangrove loss are of global concern, but more information regarding the response of below-ground carbon to disturbance or destruction is still limited. If carbon stores are highly refractory then they may remain buried even after total removal of the forest above. Alternatively they may become vulnerable to erosion and oxidation even following relatively minor disturbance (such as small-scale cutting). Sediment exposure, due to clearing of mangroves, triggers loss of C stocks in sediments through increases in the rate of organic matter decomposition (through increased nutrient cycling and microbial activities) and leaching of dissolved organic C (Couwenberg *et al.*, 2010; McLeod *et al.*, 2011). Recent estimates have indicated that sediment C stocks may decline by up to 50 % in a span of 8 years following clearing of mangrove forests (Granek and Ruttenberg, 2008; Sweetman *et al.*, 2010). This implies that total C lost through mangrove deforestation is far more than what is lost through removal of above-ground biomass alone (McLeod *et al.*, 2011).

There are only three published studies that have directly considered the impacts of tree removal on below-ground carbon storage, two reporting on the effects of hurricanes (Cahoon *et al.*, 2003; Barr *et al.*, 2012) and one on the effects of total deforestation (Lovelock *et al.*, 2011). They demonstrate that under these extreme conditions carbon losses can be large with resulting 'peat collapse' and coastal erosion. The effects of smaller impacts are unknown and there are no published works on controlled experiments on this subject. With the increasing attention being paid to avoiding deforestation by REDD schemes, it is essential that the impacts of a range of forest management scenarios are analysed to understand whether sustainable forms of use of mangrove forests are possible. Therefore, this research study documents the first controlled experiments on carbon losses and impact on sediments after small-scale cutting, such as may be typical of mangrove exploitation in the Western Indian Ocean region.

The major sources of CO_2 flux from forest soils are the autotrophic (root) respiration (R_A; from roots, mycorrhizal fungi and free-living microorganisms in the rhizosphere) and heterotrophic respiration (R_H; from decomposition of litter and soil organic matter) (Sapronov and Kuzyakov, 2007; Alongi, 2009). Each of these components plays different roles in belowground C processes: root respiration gives an indication of C input to the soil C pools, whilst heterotrophic respiration is useful in quantification of soil C budgets (Sapronov and Kuzyakov, 2007). In addition, they respond differently to changing environmental conditions and disturbance regimes (Lin *et al.*, 1999; Hogberg *et al.*, 2001; Comstedt *et al.*, 2010). The relative contributions of these sources have not been

distinguished in mangroves; such partitioning is essential to determine the impacts of degradation or destruction on the decomposition of organic material in the sediment.

However, due to methodological challenges, it is very difficult to partition soil respiration in to autotrophic and heterotrophic components (Hanson *et al.*, 2000; Epron *et al.*, 2001; Baggs, 2006; Sapronov and Kuzyakov, 2007). Various techniques that have been employed to separate the components of soil respiration can be broadly grouped in to three approaches: a) component integration [separate measurements of CO_2 flux from roots, rhizosphere and non-rhizosphere soil] (e.g. Edwards and Harris, 1977), b) root exclusion (through trenching, root removal, gap formation or tree girdling), (e.g. Hogberg *et al.*, 2001; 2009; Bhupinderpal-Singh *et al.*, 2003; Binkley *et al.*, 2006) and c) isotopic techniques (Lin and Ehleringer, 1997; Ekblad *et al.*, 2002). Another approach is the indirect estimation of root respiration, which involves regression of soil CO_2 fluxes against live root biomass (Kucera and Kirkham, 1971; Rodeghiero and Cescatti, 2006).

Each of these techniques has shortcomings as well as suitability to different ecosystems (Baggs, 2006). The main constraint to component integration is the impact of physically separating the components of the soil (litter, roots and mineral soil). The removal of litter may alter the soil water status of the soil surface and inadvertently impact on the rhizosphere processes. In addition, root specific respiration has been found to be affected by the soil CO_2 concentration and therefore, attempts to measure root respiration from isolated roots must be done under CO_2 concentrations typical of the soil atmosphere (Hanson *et al.*, 2000 and reference therein). Root exclusion involve any technique that

indirectly estimates root respiration by measuring soil respiration without roots, which is achieved by root removal (roots are excavated to a specified depth, separated from soil and the soil returned to the pit in reverse order of removal and barriers are used to prevent new root growth), trenching (roots are severed by trenching at a plot boundary, but not removed and barriers installed to prevent new root growth), gap formation (removing all the aboveground vegetation over a specified area/plot) and tree girdling (removal of the bark and phloem tissue of the stem) (e.g. Hanson *et al*., 2000; Baggs, 2006).

Root removal has advantage over the other root exclusion techniques in that, i) large amounts of roots are not left in the soil to contribute to CO_2 production through decomposition, and ii) root biomass from excavated roots can be estimated. However, a serious impediment to this technique is soil disturbance. Gap formation main constraint is the effect of aboveground vegetation removal on soil surface temperatures. Trenching and tree girdling are the most common methods used in forest ecosystems (e.g. Hogberg *et al.*, 2001; Bhupinderpal-Singh *et al.*, 2003; Binkley *et al.*, 2006; Comstedt *et al.*, 2010). However, the main disadvantages of trenching are the lateral root decomposition and the possibility of invasion of new roots below the barrier. The rationale in tree girdling approach is to stop the flow of photosynthates to the root system by the removal of the bark and phloem, while maintaining the tree canopy (Comstedt *et al.*, 2010) and therefore, since the roots are killed because of lack of carbohydrate flow, it is assumed that the CO_2 flux from the soil in girdled plots will only represent the heterotrophic component. For the tree girdling technique, the main impediment other than the contribution of dying roots to CO_2 production, is the sustained health of the trees after girdling.

Isotopic approach has advantage over the component integration and root exclusion methods because it allows the in situ separation of the components of soil respiration as well as avoiding disturbance effects and assumption of equilibrium of soil C pools common to the latter approaches (Andrews *et al.*, 1999; Hanson *et al.*, 2000; Baggs, 2006). One approach under this technique involves addition of CO_2 of known C isotopic composition to the ecosystem (which is then taken up by vegetation) and tracing it through the soil respired CO_2 (e.g. Trumbore *et al.*, 2006). Another approach is based on the change in the photosynthetic pathway, e.g. growing of C_4 plants in soils containing organic matter derived from C_3 plants and vice versa (Robinson and Scrimgeour, 1995; Ekblad *et al.*, 2002). However, the main limitation of the isotopic techniques is the complexity of the experimental set up and/or the added difficulty and cost of analytical measurements of stable or radioactive C isotopes (Hanson *et al.*, 2000; Baggs, 2006).

The regression analysis technique, which is based on the regression of CO_2 efflux against live root biomass (Kucera and Kirkham, 1971; Rodeghiero and Cescatti, 2006), can give an approximate contribution of R_A to R_S assuming spatial homogeneous R_H and no interaction between microorganisms and roots (Xu *et al.*, 2001). The R_H component is estimated from the *y*-intercept of the regression; i.e. the CO_2 efflux in the absence of roots (Kucera and Kirkham, 1971; Rodeghiero and Cescatti, 2006). The main challenges facing the regression analysis technique are the heterogeneity of soil characteristics and seasonal variations of climatic factors which influence the different components of soil respiration (Baggs, 2006, Rodeghiero and Cescatti, 2006).

Based on the nature of mangrove environment and coupled with the constraints involved in each technique, the most plausible techniques to employ in separating components of soil respiration in mangrove ecosystem are the tree girdling and the regression analysis techniques.

The present study used a controlled experiment to explore the impacts of tree removal on: a) carbon emissions from sediments, and b) surface elevation dynamics in a natural mangrove forest at Gazi bay, Kenya. In addition, it aimed to separate autotrophic and heterotrophic respiration from mangrove sediments using the girdling technique and regression modelling.

2.2   Materials and Methods

2.2.1   Study Site

The study was carried out at Gazi Bay (4^o25'S and 4° 27' S; 39^o50'E and 39° 50' E), ~ 55 km south of Mombasa, Kenya (Figure 1.2, Chapter One). Gazi Bay is a creek system with a total area of 615 ha mangrove forest (UNEP, 2001), dominated by *Rhizophora mucronata* (Lam)*, Ceriops tagal* (Perr.) C. B. Robinson and *Avicennia marina* (Forsk.) Vierh. The forest is sheltered from strong wave action by the presence of the Chale peninsula to the east and a fringing reef to the south. There are two major creeks penetrating the forest; the western creek is in the mouth of river Kidogoweni, a seasonal river, while the eastern one, Kinondo, is a tidal creek. Gazi bay has a semi-diurnal tidal regime with amplitude varying between ~ 4.0 m at spring tide and 0.70 m at neap tide (Hemminga *et al.*, 1994). High tidal flushing rates are coupled with short residence times (3–4 h), which are a function of wide

shallow entrance, lack of topographic controls and the orientation of the bay with respect to dominant water circulation patterns (Kitheka, 1997).

The long rains along the Kenyan coast occur from April to July and are associated with the southeastern monsoon (SEM) winds, while the short rains (associated with the northeast monsoon (NEM) winds) occur from October to November. The mean annual precipitation of Gazi bay ranges from 1000-1600 mm (UNEP, 1998). The bay receives freshwater from two semi-permanent rivers: Kidogoweni to the north, which discharges in to the Kidogoweni creek, and to the south, Mkurumuji river discharges freshwater to the mouth of the bay. The mangroves are not continuously under direct influence of fresh water because the two rivers that discharge into the bay are seasonal and temporal depending on the amount of rainfall inland. Ground seepage is also restricted to a few points (Tack and Polk, 1999). River discharge is important during the wet season, which enhances weak stratification in the upper parts of Kidogoweni, whereas in the dry season, well mixed homogenous water is found in most regions of the bay (Kitheka, 1997). Average sediment porewater salinity ranges from 26 to 49 ‰ with seasonal and topographic variations, the hypersaline landward sites have been shown to have porewater salinities of > 100 ‰ (Gallin *et al.*, 1989; Verheyden *et al.*, 2004; Schmitz *et al.*, 2006; Huxham *et al.*, 2010a). The annual air temperature averages 26 ^{o}C with daily variation of 24-39 ^{o}C and relative humidity averages 95 % (Kenya Meteorological Department, Mombasa).

Like most of the mangrove forests along the Kenyan coast, the mangrove forests of Gazi are licensed for harvesting of building poles (Dahdouh-Guebas *et al.*, 2000; Abuodha and

Kairo, 2001) without any management system of harvesting. As a result, some mangrove areas are either degraded or completely denuded of vegetation (Bosire *et al.*, 2003; Dahdouh-Guebas *et al.*, 2004). Despite being subjected to immense human pressures in the past, mangroves are the only natural forests in Kenya currently licensed by the Kenya Forest Service (KFS) for pole harvesting. Approximately 90 % of extracted mangrove products are for construction purposes (Dahdouh-Guebas *et al.*, 2000). The local communities neighbouring the Gazi mangroves depend heavily on mangroves for building poles and firewood.

2.2.2 Experimental Design

Ten 12 m x 12 m plots were established in March 2009 at a mid-shore level (with the height above mean sea-level ranging from 2.88 – 2.99 m) within a *Rhizophora mucronata* (**Lam**.) dominated forest. In October 2009, five plots were randomly allocated to 'treatment' and all the trees within them were girdled at ~ 20 cm above the highest prop root. Girdling is a method that has been used in a number of terrestrial forests to estimate the contribution of root respiration to total sediment gas flux. The rationale is to prevent the flow of carbohydrates from the tree canopy to their roots (thus stopping root respiration) whilst leaving the above-ground components relatively undisturbed; trees may retain foliage for many months after girdling (Hanson *et al.*, 2000; Hogberg *et al.*, 2001; 2009; Andersen *et al.*, 2005).

The other five plots served as the controls. In May 2010 all the trees in the girdled plots were cut at ~ 20 cm above the highest stilt roots and all the debris, except small fragments, was removed. The treated plots were allowed to stabilize after disturbance for a period of ~ 3 weeks, thereafter, sampling was resumed.

Plate 2.1. Girdling [a) and b)] and cutting [c) and d)] treatment carried out for the tree harvest experiment in *R. mucronata* forest at Gazi bay, Kenya

During each treatment operation seedlings and saplings < 1.5 m in height were cut down to minimize the contribution of new roots to sediment CO_2 emissions in the treated plots. Hence the experiment consisted of three sampling periods: a) baseline (pre-treatment) (June

2009 to August 2009, 84 days), b) girdled period (December 2009 to May 2010, 159 days) and c) cut period (May 2010 to April 2011, 343 days).

2.2.3 Vegetation and Environmental Attributes

Before the treatments were applied the aboveground structural attributes (stem diameter, tree height, stem density, basal area and the above- and belowground biomass) of the forest were described. For each tree (with $\geq$ 2.5 stem diameter) within each plot the stem diameter at ~ 30 cm above the highest prop root and the tree height were measured using a forester's calliper and graduated pole, respectively. From this data, the stem density, basal area and aboveground biomass (AGB) were derived. The aboveground biomass was derived from the mixed effects model (Gelman and Hill, 2007) developed for the mangrove forests of Gazi bay (R. Cohen in preparation). The aboveground tree datasets of stem diameter ($\geq$ 2.5 cm) and tree height ($\geq$ 2m) for Gazi bay mangroves (Kirui *et al.*, 2006; Kairo *et al.*, 2008; Tamooh *et al.*, 2008) were used in developing the model (R. Cohen):

LnAGB = -3.068174 + 1.77556*(lnD) + 1.2807482*(lnH)+0.30916

Where AGB = aboveground biomass, D = stem diameter and H = tree height.

Basal area (m^2) was calculated as: BA = 0.00007854 D_{130}^2 (Cintron and Schaeffer-Novelli, 1984).

The belowground biomass was estimated by the coring technique, in which four random root samples to a 60-cm depth were excavated with a corer (14.5 cm diameter) from each

plot. The samples were washed of sediments and put in labelled plastic bags for processing later in the lab. In the lab the samples were separated in to live and dead roots based on the structural integrity and signs of decomposition (McKee *et al.*, 2007b), after which they were oven-dried at 80° C to constant dry weight. The oven-dried samples of each category were weighed to the nearest 0.01 g. Other dead plant materials present were also noted.

Environmental variables such as height above sea-level and soil phyico-chemical characteristics (soil redox potential, porewater salinity and soil grain size) were assed at the initial experimental set up. The soil characteristics were also assessed during the cut period. The height above sea-level (m) for each plot was determined from measurement of height of the water column in the plots at high tide and subtracted from the high tide prediction for the day of measurement.

Each plot was divided in to four equal quarters and four surface scrapes, each at a random point in each quarter, were scooped to 1 cm depth using a 10-cm long 6 cm x 6 cm corer. The subsamples for each plot were reconstituted as one sample, mixed well in labelled airtight plastic bags and taken to the laboratory for grain size analysis. In the laboratory the samples were weighed and oven-dried at 80° C for 24 hours after which they were weighed again to determine the soil moisture (SOM) content. Twenty five (25) grams oven-dry weight of each sample was treated with 10 ml of aqueous sodium hexametaphosphate $((NaPO_3)_6)$ in a labelled beaker and subjected to a series of sieves; ranging from 63 to 500 μm mesh-size, to determine the portion of different grain sizes (i.e., < 63, 63-500 and > 500 μm particle size).

Redox potential and salinity samples were obtained from four random points in each plot at 10 and 40 cm depth using a D-section soil corer. Redox potential measurements were made using a portable redox meter as soon as the core was removed. For salinity ~ 50 g of the samples were taken for centrifuging in the laboratory to extract pore water, which was tested for salinity using a handheld refractometer.

2.2.4 Gas Fluxes and Stable Carbon Isotope Signatures

Gas flux (CO_2, CH_4) samples were collected at low tide during spring tides using six chambers per plot. Each chamber was inserted in to the sediment to ~ 5 cm, occupying an area of 0.064 m^2 and with an internal volume of 0.011 m^3. The samples from each chamber were taken 20 minutes after closure. Using a 60 ml syringe, at least 240 ml of gas sample were transferred from each chamber to labelled airtight gas-bags (Cali-5-bond gas bags, Calibrated Instruments Inc. USA). A gas sample of ambient concentration was taken from each chamber before closure; ambient air concentration samples for each plot were sampled into one gas bag.

Sediment surface temperature measurements were made beside each chamber with a temperature probe inserted to ~ 1 cm in to the sediment. Likewise, the number of crab burrows within the area enclosed by the chamber was noted. The positions of the chambers were marked for subsequent sampling and gas samples were therefore taken from the same positions in the plots at each sampling time. Pre-treatment (baseline) flux samples were collected in June, July and August 2009. Post-girdling samples were collected from

December 2009 to March 2010; whilst the post-cutting samples were taken from May 2010 to May 2011. Samples for carbon isotope analysis on CO_2 were collected during the post-treatment periods. Samples were transferred from the chambers to 12 ml pre-evacuated exetainers (Labco exetainer, Labco Ltd., High Wycombe, UK).

Gas flux samples were analysed at the Institute of Atmospheric and Environmental Sciences, University of Edinburgh, UK. For CO_2, the samples were analysed by gas chromatography (GC) using a Perkin Elmer Model 310 with a thermal conductivity detector (TCD). Analysis for CH_4 was done using GC (Hewlett Packard 5890 GC, Hewlett Packard Ltd, Stockport, Cheshire, UK) equipped with a flame ionisation detector (FID) and a digital integrator. The carbon isotope analysis samples were transferred to Department of Earth and Environmental Sciences, KU Leuven, Belgium and analysed using a Sercon 20-20 isotope ratio mass spectrometer (IRMS) interfaced with a cryofocussing unit.

Samples for sediment analysis were taken from each plot in February 2010 and August 2012. A sediment core was taken in the centre of the plot using a plastic corer (diameter 6 cm, length 3 m) and subsamples were taken with a stainless steel core (diameter 3 cm, length 5 cm) at depths of 0, 2, 4, 8, 10, 20, 30 and 40 cm (February 2010) and depth intervals of 0, 10, 20, 30, 50 and 100 cm (August 2012). To minimize compression of the sediment the coring was done in a series of stages according to the depth profiles for subsampling. Sediment samples were oven-dried at 80 ^{o}C to constant dry weight and bulk density was determined. The oven-dried samples were transferred to the Department of Earth and Environmental Sciences, KU Leuven, Belgium for analysis of sediment total

organic carbon (TOC), total nitrogen (TN) and $\delta^{13}C$ of SOC. The concentrations of SOC, total N, and $\delta^{13}C$ values of SOC were measured on subsamples weighed into Ag cups, acifidied with dilute HCl, and analysed with a Thermo Flash HT elemental analyser coupled to a Thermo Delta V Advantage IRMS (Conflo IV interface). Data were calibrated with IAEA-C6, and internally calibrated acetanilide and leucine. From the sediment bulk density and OC content, the carbon density and hence the soil carbon stocks down to 100 cm were derived for the control and treated plots.

At the end of the sampling period, all roots beneath each chamber in the control plots were excavated to a depth of 60 cm, washed of sediments and separated in to live roots and dead plant materials. The samples were then oven-dried at 80° C to constant dry weight and oven-dry weight recorded to 0.01 g. Samples of live roots were transferred to the Institute of Atmospheric and Environmental Sciences, University of Edinburgh, UK, for analysis of elemental carbon and $\delta^{13}C$ of mangrove roots.

2.2.5 Root Decomposition

In September 2010, live roots were excavated within the *R. mucronata* forest contiguous to the experimental plots. Nylon mesh (1mm) bags each containing ~ 30 g fresh roots were buried to ~ 20 cm depth at six random points within each plot. Three bags were retrieved from each plot at 156 days after burial, whilst the other three were retrieved 267 days after burial. The contents of each root-bag were rinsed and oven-dried at 80° C for 24 h before weighing. The rate of root decay (% weight loss day^{-1}) was calculated as the percentage weight loss divided by the number of days buried, using wet-dry weight conversion factors

derived from representative samples of live roots oven-dried at 80° C until constant dry weight. The rate of root decay (% weight loss day^{-1}) was calculated as the percentage weight loss divided by the number of days buried.

2.2.6   Surface Elevation and Sediment Accretion

Surface elevation dynamics were monitored using surface elevation stations (SES), comprising of two stainless steel rods (6 mm by 1 m) and a horizon marker (kaolin) set up in a 20 cm x 20 cm quadrat in each plot. The rods were installed leaving a height of 20 cm above the ground. To test the efficacy of the 1 m rods (which may give readings affected by movements of the soil profile below the depth of 80 cm), a set of 3 m stainless steel rods (6 mm diameter) were introduced on the 539th day after the experiment was established. During the installation of the 3-m rods, the height readings for the 1-m rods were noted for each plot and all the rods were set to the same level (~ 15 cm above the ground level) using a spirit level based on the smallest height of the 1-m rods' immediate readings before the installation the 3-m ones (Figure 2.1). Height measurements from the ground surface to heights of the rods were made at seven points along a wooden board placed across each set of rods (Figure 2.1). Sediment accretion was determined from measurements of height above the horizon marker. In each quadrat, at least four soil blocks of 2 cm x 2 cm were carefully removed with a sharp knife, the height of sediment above the horizon marker was measured to the nearest 1 mm and the block was then carefully replaced in its original position. This design allows the separation of total surface elevation/subsidence (which depends on both the accretion of new sediments and on below-ground processes such as root growth) from accretion/erosion (Cahoon *et al.*, 2003).
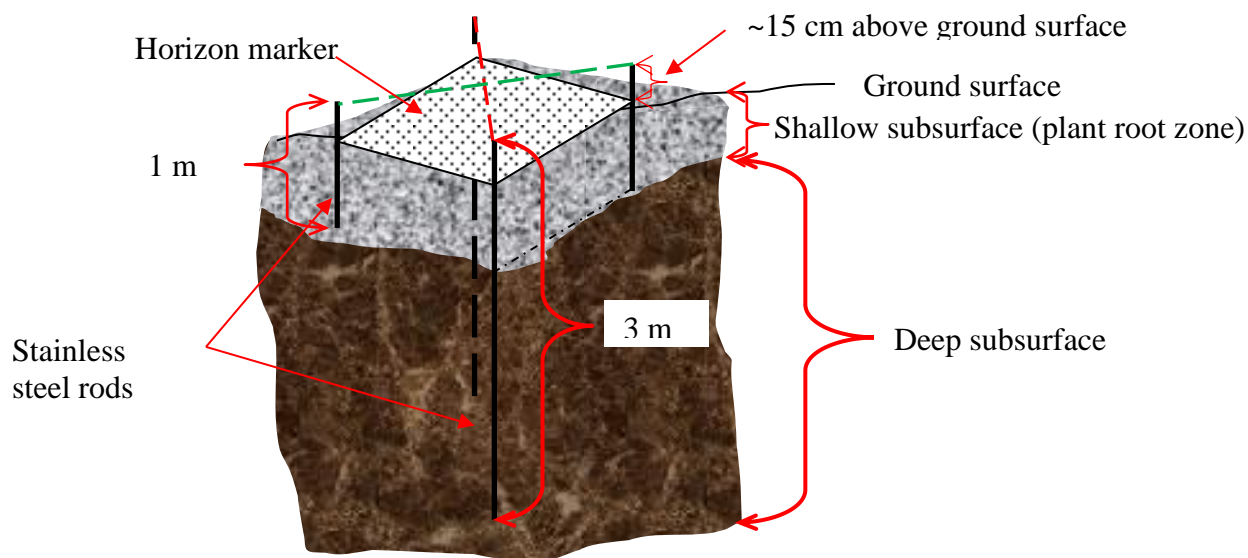
Figure 2.1. Illustration of the installation of surface elevation station (SES) in *R. mucronata* forest at Gazi bay, Kenya. The dashed red and green lines show points along which measurements are taken for long and short rods, respectively. During the installation of the 3-m rods all the rods were re-set to the same level (~ 15 cm above the ground) using a spirit level based on the least height of the previous reading of the 1-m rods.

Plate 2.2. Surface elevation station measurements for a) surface elevation and b) sediment accretion in *R. mucronata* forest at Gazi bay, Kenya.

2.2.7   Statistical Analysis

The data for CO_2 were log-transformed and analysis for each gas was executed using MINITAB 14 software package. The gas flux values for each chamber were pooled across for each period (baseline, girdled and cut). For each period, nested ANOVA was carried out for each gas, with plots nested in treatment and sediment surface temperature and crab burrows as covariates. Estimates for $\delta^{13}C$ of sediment respired CO_2 were derived from the Miller-Tans mixing model combined with geometric regression (Miller and Tans, 2003). Kayler *et al*. (2010) found that the combination of geometric regression and Miller-Tans mixing model gave the most accurate and precise estimate of $\delta^{13}C_S$ (S = sediment respired CO_2). The gas mixing models are based on the conservation of mass given as (Miller and Tans, 2003):

$$\delta_{obs}[CO_2]_{obs} = \delta_{bg}[CO_2]_{bg} + \delta_s[CO_2]_s$$

This equation describes the gas observed (obs) as coming from two sources; background atmosphere (bg) and source of respiration (s); where δ refers to the isotopic value of each component. Details of the Miller-Tans mixing model combined with geometric regression are discussed by Kayler *et al*. (2010). For each plot the $\delta^{13}C$ of the respired CO_2 were pooled and the difference between the control and treated plots was tested using two-sample t-tests.

To examine the autotrophic contribution to sediment fluxes, stepwise multiple regressions (forward and backward elimination) were performed, with the final CO_2 fluxes measured in each control chamber in April 2011 as the dependent variable and the live root biomass, sediment surface temperature and crab burrows for each chamber as the independent variables. The equation takes the form of *y = k + a*roots + b*temperature + c*burrows*; where *k* = constant, *a*, *b* and *c* are the coefficients of the estimators. The number of crab burrows was not significant, and hence this term was omitted from the equation. The significant factors were used in estimating the autotrophic respiration from the final CO_2 flux data. First, the heterotrophic respiration (R_H) was calculated as the value of the '*y*' when live root biomass = 0; i.e. *R_H = k + b*temperature*. Then the autotrophic respiration (R_A) was obtained as the difference between total sediment respiration (R_S) and the heterotrophic component (R_H) and expressed as a percentage of R_S (i.e. %R_A = (R_S–R_H)/R_H*100). To estimate the contribution of R_A across the entire sampling period the equation was applied to the CO_2 flux data together with the sediment surface temperature

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for each control chamber at each sampling time. The mean R_A contribution across the sampling period was then compared with that obtained from the final sampling time.

The difference in the rates of root decomposition in the control and treated plots was tested using a two-sample t-test. Cumulative elevation change (change from the baseline data) for each sampling time was determined for each plot. In order to test the effects due to treatment (girdling and cutting), the mean values during the baseline period for each plot were used as a benchmark for determining cumulative elevation during the treatment periods.

The additional C emission due to treatment was estimated as the area under area curve based on trapezoidal rule of an integral function (Cerone and Dragomir, 2000). Since the graph of this function normally assumes an irregularly shape, the area can be divided in to small trapezoidal shapes and the total area calculated as the sum of the areas of all the trapezia making up the shape (Cerone and Dragomir, 2000):

$$AUC = \sum_{i=1}^{n} \frac{(m_i + m_{i+1})}{2} t_i$$

Where AUC = area under curve, n = number of measurements, m = individual measurements and t = time difference between any consecutive measurements.

Soil carbon concentration (gC cm^{-3}) was calculated as the product of bulk density (BD) and % organic C content of the soil. Subsequently, the soil carbon stocks down to a depth of 100 cm for each treatment was calculated as the product of carbon concentration and the depth and expressed as tC ha^{-1}:

$$C_S = C_C * (100 + E_c);$$

Where, C_S = soil C stocks, C_C = C concentration and E_c = elevation change. Since the control plots gained 1.1 cm and the treated plots lost 5.1 cm in surface elevation (*see* Figure 2.7, Results), the depth for each treatment was adjusted to reflect these changes, i.e. 100 + E_c = 101.1 and 94.9 cm for control and treated plots, respectively.

2.3   Results

2.3.1   Vegetation and Environmental Attributes

The vegetation and environmental characteristics at the beginning of the experiment are given in Table 2.1. The bulk of belowground biomass during the initial (2009) and final (2011) sampling was in the dead roots, which increased significantly in the control plots in over 2 years (paired t-test; t = -3.2, P = 0.03). On the other hand the increase in the dead root biomass in the cut plots approached significance when compared with that observed in the same plots (43.0 ± 21.5 t ha^{-1}) before treatment (paired t-test t = -2.75, P = 0.051). Other dead plant materials comprised 13.3 and 4.3 % of the total belowground necromass in the control and cut plots, respectively. The plant roots had a similar stable carbon isotope signature to that of the soil carbon (Table 2.1). The control and treated plots had similar soil moisture content, bulk densities, organic carbon concentration and stable C isotope signatures. Though the soil carbon stocks in the treated plots was less than that of the controls, the difference was not significant (t-test, t = 0.88, P = 0.407).

Table 2.1. Vegetation and environmental attributes in *R. mucronata* forest at Gazi bay, Kenya. Values are means±95% CI, OC_R represents elemental carbon content of roots, $\delta^{13}C_R$ and $\delta^{13}C_S$ represent $\delta^{13}C$ values of root and soil TOC, respectively and TN and TOC are total nitrogen and organic carbon content of the soil, respectively.

Variable	Baseline (n = 10)	Control (n = 5)	Treated (n = 5)
Stand density (stems ha^{-1})	4417 ± 647		
Tree height (m)	5.3 ± 0.9		
Basal Area (m^2 ha^{-1})	14.5 ± 2.1		
AGB (t ha^{-1})	85.0 ± 6.2		
BGB (t ha^{-1}) (*a*) *Live roots*	33.1 ± 16.2	21.3 ± 11.4	
(*b*) *Necromass* (i) Dead roots	40.2 ± 12.8	89.2 ± 28.8	73.3 ± 5.3
ii) Other dead plant materials	7.5 ± 3.5	10.5 ± 4.7	3.3 ± 1.6
% OC_R	37.2 ± 1.7		-
d$^{13}C_R$ (‰)	-27.0 ± 0.3		-
Soil moisture content (%)	44.3 ± 0.9	46.5 ± 4.0	42.0 ± 5.7
Salinity (‰) (a) 10 cm depth	46.5 ± 1.7	36.6 ± 2.6	36.2 ± 2.6
(b) 40 cm depth	46.6 ± 1.0	41.2 ± 1.6	35.0 ± 4.0
Redox potential (mV) (a) 10 cm depth	-53.6 ± 74.6	29.9 ± 94.1	-3.9 ± 57.9
(b) 40 cm depth	-159.1 ± 109.6	-112.2 ± 163.5	-96.5 ± 130.3
Grain size (%) a) < 63μm	16.3 ± 1.3		
b) 63-500 μm	60.5 ± 0.3		
c) > 500 μm	23.2 ± 1.6		
Bulk Density (g cm^{-3})		0.84 ± 0.08	0.88 ± 0.10
Soil C concentration (gC cm^{-3})		0.052 ± 0.008	0.052 ± 0.008
% N		0.38 ± 0.04	0.36 ± 0.11
TOC/TN		18.59 ± 0.8	17.6 ± 0.7
d$^{13}C_S$ (‰)		-27.2 ± 0.2	-27.4 ± 0.1
Soil C stocks* (tC ha^{-1})		524.1 ± 62.7	488.4 ± 48.4

*Soil C stocks down to 1 m depth (calculated as C concentration (g cm^{-3}) x depth (cm) and expressed as tC ha^{-1})

2.3.2   Carbon Fluxes and Stable Carbon Isotope Analysis
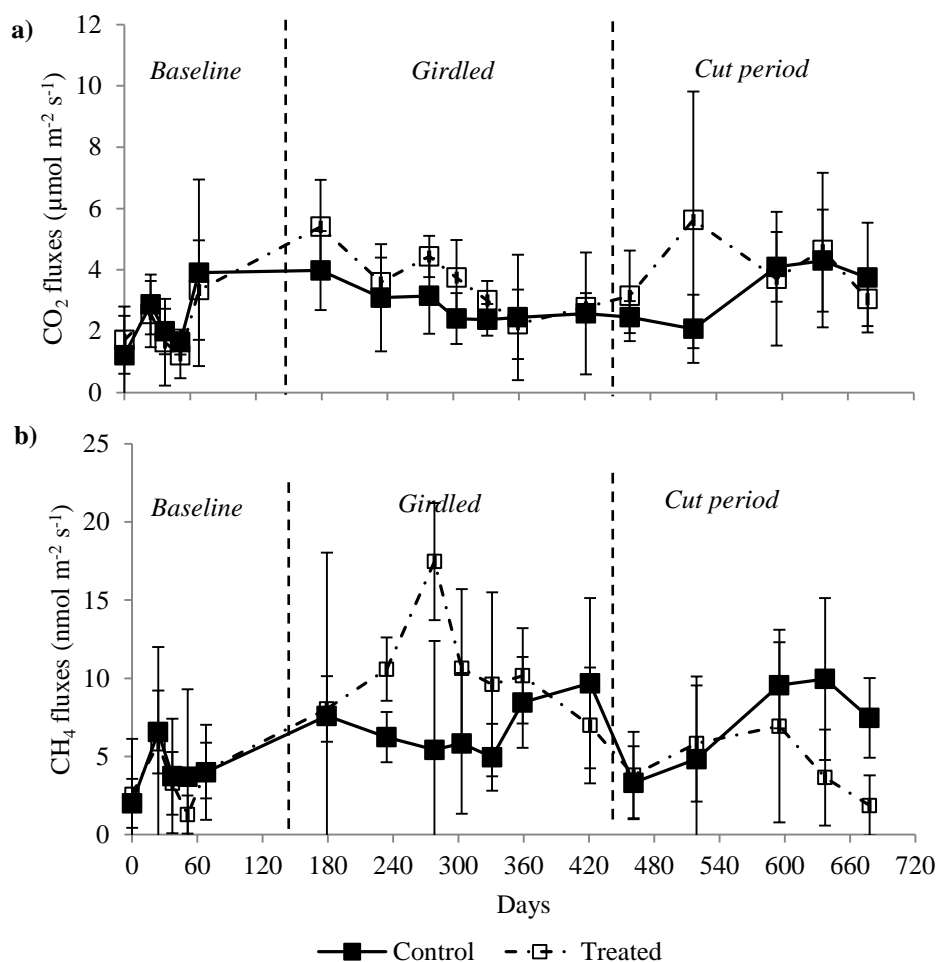
Figure 2.2. Mean (±95% CI) Carbon emissions: a) CO_2 and b) CH_4 emissions in control (solid line with filled squares) and treated plots (broken line with open squares) in *R. mucronata* forest at Gazi bay Kenya. Vertical broken lines indicate periods when trees were girdled and cut in the treatment plots. Baseline, girdled and cut periods sampling was done from June 2009 to August 2009 (84 days), December 2009 to May 2010 (189 days) and May 2010 to April 2011 (434 days), respectively.

Approximately 30 days after girdling CO_2 emissions in treated plots increased and remained higher than that in the controls throughout the girdled period (Figure 2.2a). For the first two months after cutting the CO_2 emissions in the treated plots fell to the levels of the controls, but increased again for three months after cutting. However, by the end of the sampling period, CO_2 emissions had dropped to similar levels as those in the controls (3.0 ± 0.6 vs 3.7 ± 1.3 µmol m^{-2} s^{-1}, respectively; Figure 2.2a). Methane emissions were highly variable and increased in the treated plots during the girdled period only (Figure 2.2b).
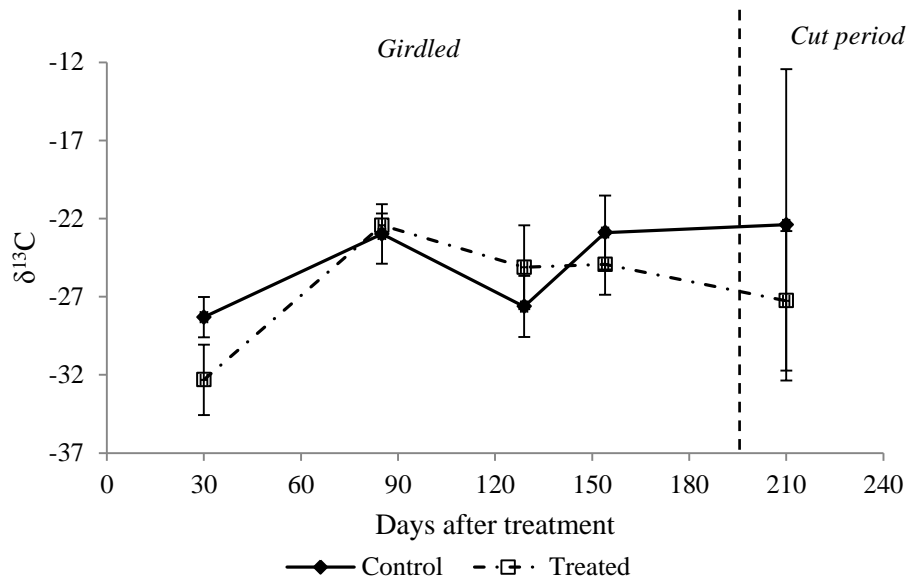
Figure 2.3. Trends in $\delta^{13}C$ of sediment respired CO_2 in the control and treated plots in *R. mucronata* forest at Gazi bay, Kenya. Error bars are 95% CI, vertical broken line indicates when the trees were cut in treatment plots.

Table 2.2. Nested design ANOVA for carbon fluxes in *R. mucronata* forest at Gazi bay, Kenya: the data for CO_2 were log-transformed

Period	Variable	Source	DF	MS	F	P
Girdled	CO_2	Temperature	1	0.017	0.420	0.518
		Burrows	1	0.017	0.45	0.506
		Treatment	1	0.152	4.73	0.036
		Plot (Treatment)	8	0.025	0.64	0.736
		Error	48	0.039		
	CH_4	Tempt	1	46.140	2.4	0.128
		Burrows	1	2.660	0.14	0.712
		Treatment	1	745.800	20.04	0.000
		Plot (Treatment)	8	55.700	2.9	0.01
		Error	48	19.230		
Cut	CO_2	Tempt	1	0.005	0.16	0.695
		Burrows	1	0.044	1.26	0.267
		Treatment	1	0.001	0.02	0.897
		Plot (Treatment)	8	0.028	0.81	0.6
		Error	48	0.035		
	CH_4	Tempt	1	24.758	3.43	0.07
		Burrows	1	5.73	0.79	0.378
		Treatment	1	1.458	0.19	0.667
		Plot (Treatment)	8	10.834	1.5	0.182
		Error	48	7.225		

At ~ 30 days after girdling, the CO_2 flux from the treated plots was significantly more depleted in ^{13}C than in the controls; this was also the case at 20 days after cutting (Figure 2.3). Throughout the treatment period, the mean sediment temperature in the treated plots was higher than that of control plots by values ranging from 0.9 to 5.8 °C. The overall mean CO_2 and CH_4 emissions during the girdled period were significantly higher in treated plots than in the controls. However, there was no significant difference between the treatments for both gases during the cut period (Nested ANOVA, Table 2.2).

Contribution of root respiration to total sediment respiration

Girdling was not effective in separating the components of soil respiration since the girdled trees began to lose leaves and died three months after girdling, which was much faster than what was observed in terrestrial trees (Andersen *et al.*, 2005). Therefore, regression technique, an indirect method of estimating autotrophic respiration, was used (Hanson *et al.*, 2000). The regression of CO_2 fluxes measured at the final sampling (April 2011) against live root biomass combined with sediment surface temperature was significant:

Multiple regression: $lnCO_2 = -3.093 + 0.0002*$live root biomass $+ 0.127*$temperature; $R^2 = 0.37$; $P = 0.044$, 0.011 and 0.012 for the constant, live root biomass and sediment temperature, respectively.

Heterotrophic respiration (R_H) for CO_2 emission values measured at the final sampling was calculated by applying the equation above, while setting the value of root biomass to zero. Autotrophic respiration (R_A), obtained by subtracting the values for R_H from the measured total sediment respiration (R_S), contributed a mean (±95 % CI) of 41.5 ± 11.8 % to R_S at the final sampling. Across the entire sampling period, R_A contributed an average of 40.5 ± 7.0 % to R_S, which was not significantly different from that obtained at the final sampling (t-test, t $= -0.16$, $P = 0.874$).The partitioning of the components of total R_S in the control plots allowed a comparison of the CO_2 fluxes in the treated plots with R_H in the control plots. It was evident that sediment respiration was higher in the treated by 0.6 to 3.6 CO_2 µmol s^{-1} m^{-2} than the R_H in the control plots throughout the treatment period (Figure 2.4)
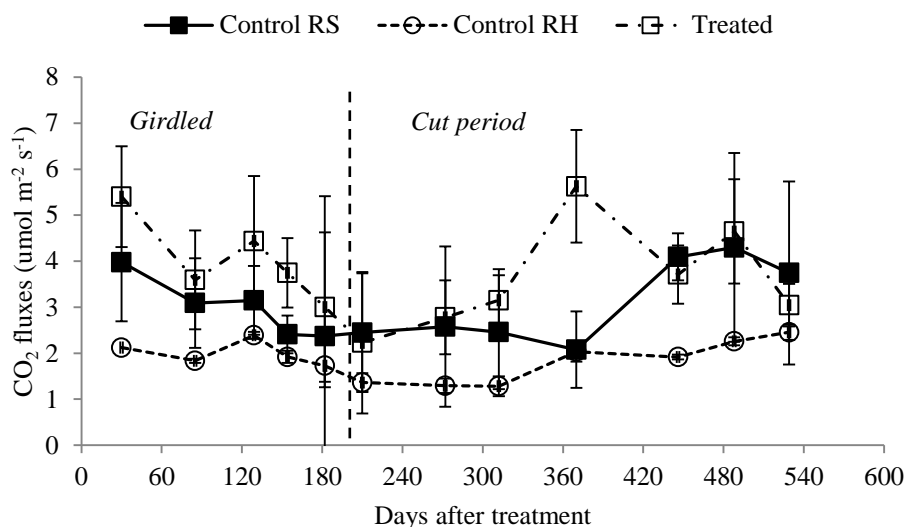
Figure 2.4. Mean (±95% CI) fluxes of total soil respiration (R_S) in control plots (solid line with filled squares), heterotrophic respiration (R_H) in control plots (dashed line with open circles) and CO_2 emissions from treated plots (broken line with open squares) during treated periods in *R. mucronata* forest at Gazi bay, Kenya

2.3.3 Root Decomposition

Rates of root decomposition were < 0.2 % dry weight loss day[-1] for both control and treated plots at 270 days after burial (Figure 2.5). The difference in the rates of decomposition between the treated and control plots was significant at 270 days after burial (t-test, t = -2.06, P = 0.049). The trend in the root decomposition rates in the treated plots indicated that it was increasing with time, while those in the control plots remained relatively constant after 150 days at 0.16 % dry weight loss day[-1].
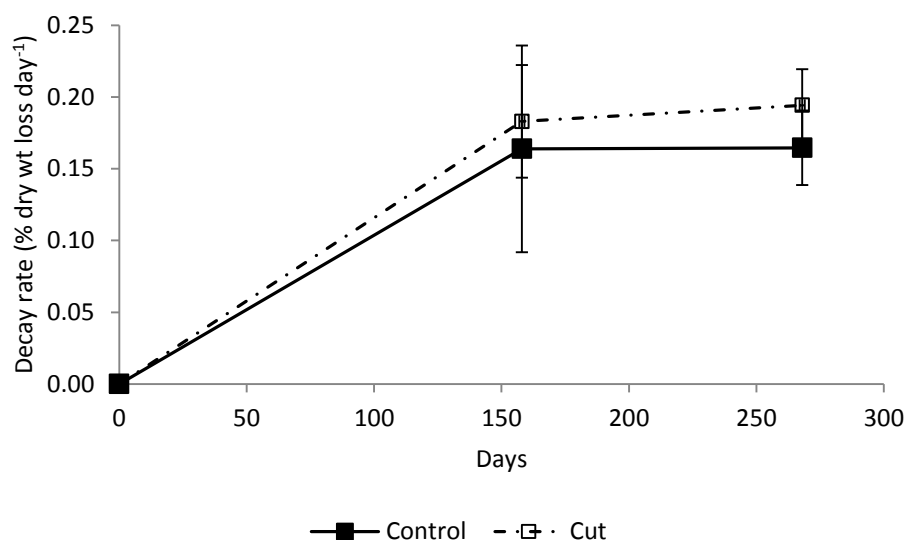
Figure 2.5. Rates of root decomposition in control (solid line with filled symbols) and cut (broken line with open symbols) plots in *R. mucronata* forest at Gazi bay, Kenya: error bars are 95 % CI.

2.3.4   Surface Elevation and Sediment Accretion

At the conclusion of monitoring after 760 days the control plots gained mean surface elevation of $+11.1 \pm 10.5$ mm at a mean rate of $+4.2 \pm 1.4$ mm yr^{-1}, while the treatment plots showed a subsidence of -51.3 ± 12.0 mm at a mean rate of -32.1 ± 8.4 mm yr^{-1}) (Figure 2.5). Measurements from the two sets of rods of different lengths for each treatment did not significantly vary, hence there was no evidence of surface elevation changes extending deeper than 80 cm [t-test; $t = -0.82$, $P = 0.439$ (control) and $t = -0.40$, $P = 0.703$ (cut), Figure 2.6].
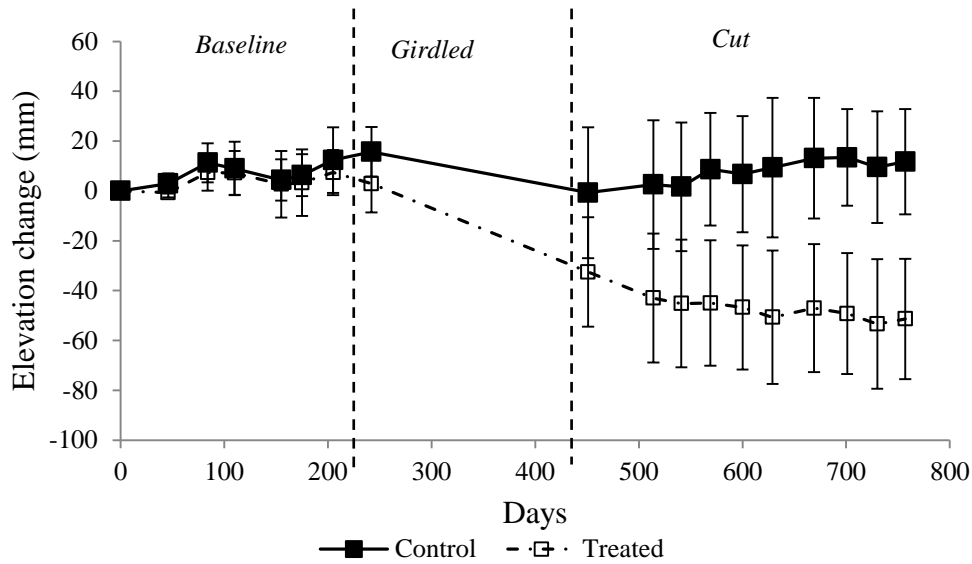
Figure 2.6. Trends in surface elevation change in control and treated plots in *R. mucronata* forest at Gazi bay, Kenya. Error bars are 95% CI. Vertical broken lines indicate periods when trees were girdled and cut in the treatment plots.

For a period of 180 days after setting up of horizon marker, both the control and treated plots experienced similar trends in sediment accretion: ranging between 5.5 to 7.5 mm (controls, mean 6.5 ± 1.8 mm) and 6.0 to 12.0 mm (treated, mean 8.1 ± 4.2 mm) (Figure 2.7). When extrapolated to annual rates, these values equated to mean (± 95% CI) rates of 12.6 ± 3.4 and 15.8 ± 8.1 mm yr^{-1} for controls and treated, respectively. Disturbance of the horizon marker by crab activities in the control plots did not allow further monitoring beyond six months after set up.
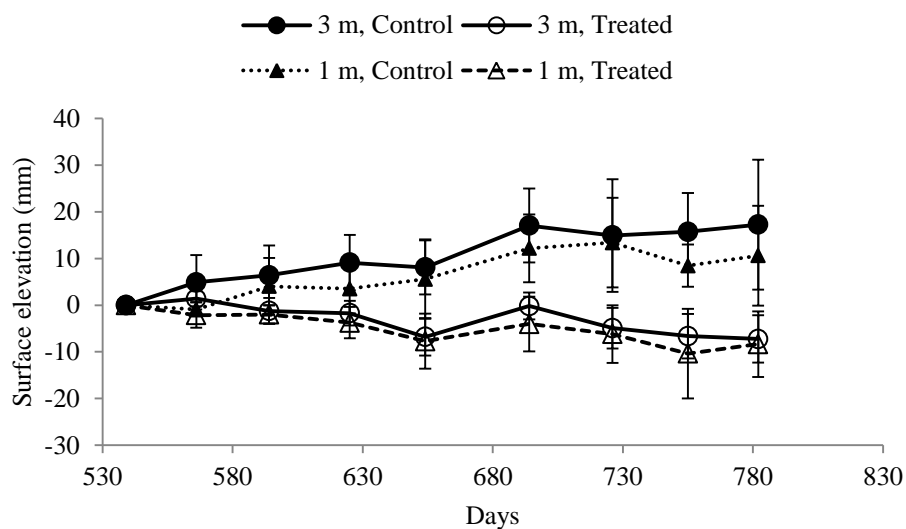
Figure 2.7. Trends in surface elevation dynamics as measured using different rod lengths in *R. mucronata* forest at Gazi bay, Kenya; 1 m (dashed lines) and 3 m (solid lines), filled and open symbols represent control and cut plots, respectively and error bars are 95% CI
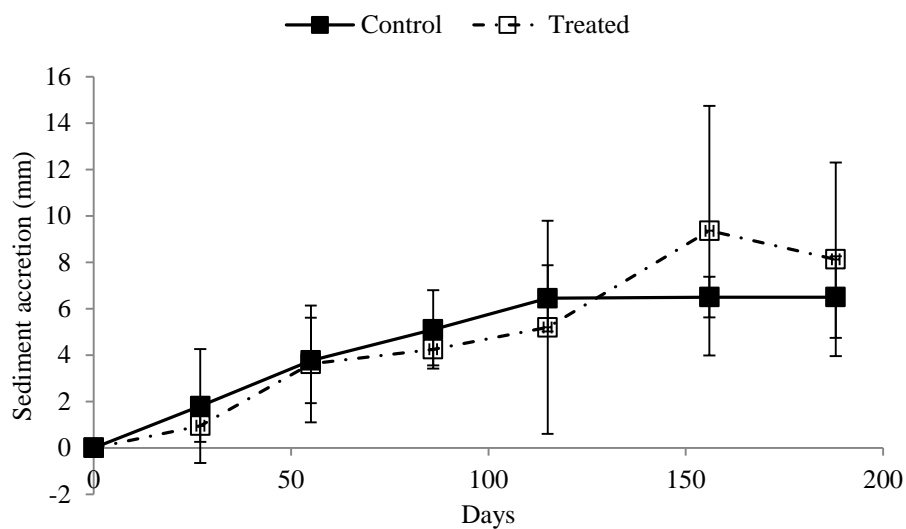
Figure 2.8. Cumulative sediment accretion in control (solid line) and cut (dashed line) plots in *R. mucronata* forest at Gazi bay, Kenya; values are means ± 95% CI

2.4 Discussion

2.4.1 Carbon Fluxes and Stable Carbon Isotope Analysis

CO_2 emissions in the treated plots exceeded those in the control plots by 14.2 ± 10.3 tCO_2 ha^{-1} over a period of 530 days (~1.5 yrs) at an average rate of 9.8 ± 7.1 tCO_2 ha^{-1} yr^{-1}. These values equated to 36.7 ± 10.7 tCO_2 ha^{-1} (mean rate = 25.3 ± 7.4 tCO_2 ha^{-1} yr^{-1}) when only heterotrophic respiration (R_H) in control plots was considered (Figure 2.8). The treatment induced CO_2 emission values reported here are similar to those reported for hurricane damaged forests in Honduras within a similar period of time (Cahoon *et al.*, 2003) and for shrimp pond modified sites in Australia (Burford and Longmore, 2001), but were by far less than the values reported 1 year after large-scale clearing of mangroves in Belize (Lovelock *et al.*, 2011) (Table 2.3). Much of the C loss occurred within the first year after treatment (mean rates of 13.22 ± 9.71 and 7.86 ± 6.77 tCO_2 ha^{-1} yr^{-1} during the girdled and cut periods, respectively) and by ~ 1.5 years, the C losses induced by treatment began to drop, indicating that the rate of root decomposition was diminishing. A similar pattern was recorded in clear-cut mangroves in Belize, in which the C emissions in disturbed areas declined with time, in which the CO_2 emissions due to destruction of canopy dropped from 106 to 29 tCO_2 ha^{-1} yr^{-1} 20 years after clearing (Lovelock *et al.*, 2011).

Table 2.3. Estimates of CO_2 emissions in disturbed mangrove forests

Location	Characteristics	Modification	CO_2 efflux (tCO$_2$ ha^{-1} yr^{-1})	Period after disturbance (years)	Method	Reference
Kenya	Muddy substrate, basin-creek setting	Small-scale cutting	9.8 (vs *R$_S$) 25 (vs R$_H$)	1.5	CO_2 efflux	This study
Belize	Peaty soils, carbonate setting	Large scale clearing	106 29	1 20	CO_2 efflux	Lovelock *et al.* 2011
Honduras	Peaty soils, oceanic setting	Hurricane damage	17.5 (2.2-50)	1	Inferred from peat collapse	Cahoon *et al.* 2003
Australia	Mangrove-lined tidal creek and river mouth	Shrimp pond	32		CO_2 efflux	Burford and Longmore 2001

*C emissions attributed to cutting as compared to the total sediment respiration (R$_S$) and heterotrophic respiration (R$_H$) in control plots, respectively.

The enhanced C emissions from treated plots were likely due to decomposition of labile root materials. However there was evidence in study site that decomposition of sediment organic carbon (SOC) - not only newly-killed root material - was enhanced by treatment, and that rates of SOC decomposition might be increasing with time. Buried root bags recorded significantly higher rates of decomposition in treated plots (0.19 ± 0.02 vs 0.16 ± 0.02 % dry weight loss day^{-1}, respectively) with most of the difference occurring after the first set of root bags were retrieved (150 days after burial). This was probably due to enhanced sediment surface temperatures in the cut plots due to canopy removal, since the treated plots experienced increase in sediment surface temperatures by 0.8 to 5.9 ^{o}C compared to the control plots. Therefore, these results highlight the potential impact of physico-chemical changes on C losses in cut forests which are separate from and additional to the losses from root death per se.

Although estimates from this study suggest high rates of below-ground C loss caused by tree death (similar to those seen following much larger impacts such as hurricanes) they are likely to represent an underestimate, at least for a number of reasons. 1) The use of sediment surface measurements of C efflux does not account for below-ground, lateral flows of carbon as dissolved inorganic carbon (DIC) (Bouillon *et al.*, 2008; Kristensen *et al.*, 2008a; Alongi *et al.*, 2012), 2) measurements were made at low spring tides when the sediment were exposed for a limited period of time than during neap tides and 3) the nature of the aboveground roots of the Rhizophora trees did not allow the chamber technique to incorporate these biogenic structures, which have been shown to be conduit of C efflux (Kristensen *et al.*, 2008b). Analysis of DIC in mangrove sediment porewater and in waters

in channels during ebb flow give similar results, suggesting that a significant amount of C produced during microbial mineralization is exported from the mangrove ecosystem as DIC (e.g. Bouillon *et al.*, 2008). Unlike for the terrestrial ecosystems, where lateral leakage of dissolved inorganic C is negligible as to warrant the uncertainty in estimation of C efflux from the soil using the surface measurements (Trumbore, 2006), such a case may not apply to the mangrove ecosystems where there is considerable export of C by tides (Bouillon *et al.*, 2008; Miyajima *et al.*, 2009). Therefore, to accurately estimate C production from mangrove sediments the sediment surface C efflux measurements need to be complimented by estimates of lateral flow of DIC and C efflux during inundated conditions.

CH_4 emissions were significantly enhanced during the girdled period, possibly because of the addition of easily fermentable substrates (Blodau, 2002; Goreau and de Mello, 2007; Kristensen, 2007) from possibly from dying fine roots but also from increased leaf litter induced by girdling. Girdling rapidly subjected mangrove trees to a lot of stress, since they started shedding leaves immediately and by the fourth month after girdling all the trees in the treated plots were dead. This rapid response to girdling was unexpected compared with the slower responses (of up to 2 years) found in terrestrial studies (Edwards and Ross-Todd, 1979) – in the absence of any previous girdling work on mangrove trees it was expected that the trees would maintain their canopy cover for longer than they did. However, emissions in both treatment periods, 0.7 – 1.5 (girdled) and 0.2 – 0.9 mmol m^{-2} d^{-1} (cut), did not exceed those reported for a number of pristine mangrove forests worldwide, 0.01 – 5.0 mmol m^{-2} d^{-1} (Kristensen, 2007 and references therein). Sediment respired CO_2 collected shortly after girdling showed significant depletion in ^{13}C (Fig. 2.3; -32.3 ‰). Such depleted

signatures are unlikely to arise from respiration of existing organic matter alone, as here $\delta^{13}C$ would be similar to the control. Rather, as coincident with increased CH_4 emissions, the most parsimonious explanation is that oxidation of methane comprised a component of the CO_2 efflux. If $\delta^{13}C$ of methane was typical of marine environments, i.e. -60 ‰ (Reeburgh, 2007), then the measured ^{13}C-depletion would represent an additional 12% CO_2 contribution from methane oxidation.
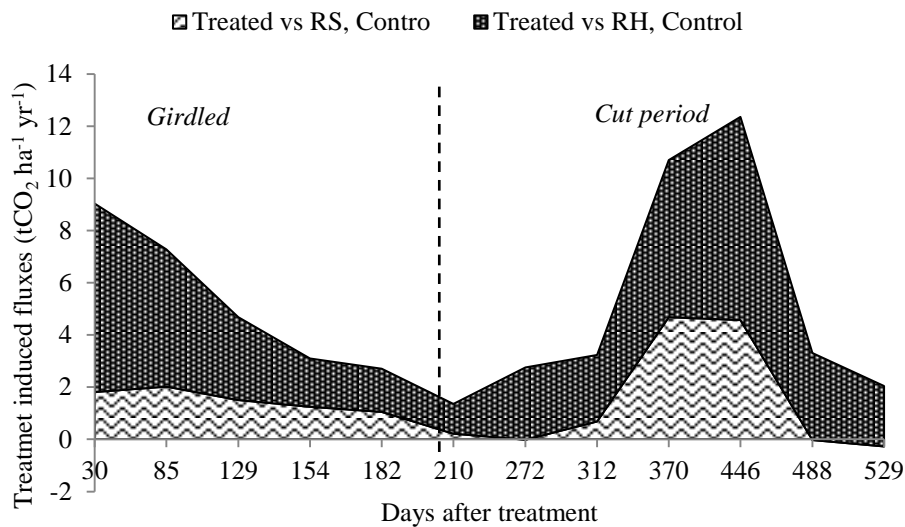
Figure 2.8. Area under curve showing the additional C emissions induced by treatment in *R. mucronata* forest at Gazi bay, Kenya: R_S and R_H refer to the total and heterotrophic respiration in the control plots, respectively.

The contribution of root respiration to total sediment respiration was 40.5±6.4 % (range: 31.2-50.0 %), which was similar to the values reported for temperate vegetated peatlands; 35-57 % (Crow and Wieder, 2005). The contribution of root respiration to total soil respiration in forest ecosystems averages at 48 %, though varying widely between 10 to 90

% (Hanson *et al.*, 2000; Baggs, 2006). Most of the uncertainties associated to the estimation of root respiration are attributed to methodological challenges (Baggs, 2006). Though the estimates provided here are within the range of those found in vegetated peatlands, the estimation did not take in to account the C loss through lateral exports by tides. In addition, the regression analysis technique used was based on one sampling point and extrapolating to cover the entire sampling period could possibly propagate additional uncertainties.

2.4.2   Surface Elevation and Sediment Accretion

Tree mortality induced a significant subsidence. This was likely due to soil collapse resulting from soil organic matter decomposition and probably collapse of arenchymatic tissues in dying roots, exacerbated by absence of growth of new roots. Sediment consolidation and/or compaction due to consolidation of air spaces might have also contributed to this. This is supported by a slightly higher bulk density (BD) in the cut plots than that of control plots (Table 2.1). The treated and control plots experienced similar rates of sediment accretion (t-test; t = 2.2, P = 0.67) and hence erosion being a factor in subsidence is ruled out. Therefore, loss of C due to enhanced organic matter decomposition was the probable cause of the loss of elevation in the treated plots. The subsidence of ~ -50 mm in the treated plots resulted in a significant difference in total soil carbon between the treatments, with a total of up to 35 tC ha^{-1} lost compared to controls (Table 2.1, Figure 2.8).

The rate of subsidence recorded here was surprisingly high. The small-scale experimental cutting caused faster subsidence than that found in hurricane-impacted basin mangroves in

Honduras over a similar period of time; - 32 vs – 11 mm yr^{-1} (Cahoon *et al.*, 2003). The probable discrepancy could be attributed to site characteristics; the Honduras mangroves, being in oceanic settings are likely to have compact autochtonous sediments (Cahoon *et al.*, 2003), while the mangrove sediments from this study site are composed of loose muddy substrate, partly of allochtonous origin. Simulations of hurricane impacts on mangrove forests have indicated subsidence of -37 mm yr^{-1} in 2 yrs after the storms (Cahoon *et al.*, 2003); which is similar to what is reported in the present study. However, Cahoon *et al.* (2003) indicated that the rate of subsidence would reduce to -7 mm yr^{-1} 8 years after the impact.

2.5 Conclusions

Mangroves in Kenya experience 0.7% loss of areal coverage per year (Kirui *et al.*, 2012). The data reported here suggest that such losses would translate to enhanced carbon fluxes from belowground sources of 3711.9 tCO$_2$ yr^{-1} (i.e. 9.8tCO$_2$ ha^{-1} yr^{-1} * 54000 ha * 0.7/100). However, this is likely an underestimate because C losses in the present study were quantified from only surface fluxes of CO$_2$, and therefore ignored possible lateral flows of carbon in DIC.

These results demonstrate that even small scale cutting of mangroves can imply significant losses of below-ground carbon and surface elevation, with the risks that the latter brings of increased inundation and erosion. This raises important considerations for managers concerned with trade-offs between different ecosystem services. Based on the projection of wood supply and demand, the Kenyan forest sector is expected to experience a deficit of

6.8 million m³ of wood by the year 2020 (MENR, 1994). Mangroves have traditionally provided most of the wood for building along the Kenyan coast and there are strong arguments for using the forests for wood production. However management plans for the forests need to take in to account the trade-offs between sufficient supplies of wood and the possibility of enhanced sediment C efflux with the loss of carbon stores that implies. Currently, the harvesting system employed in pole extraction in the region is the selective technique, in which only poles fit for construction are harvested, which has led to decrease of good quality poles (Dahdouh-Guebas *et al.*, 2000; 2004). Mangrove forestry is one of the options that might be considered. However, from these results, it is evident that there is carbon loss to the atmosphere and significant subsidence in mangrove sediment surface after tree removal. These estimates of carbon loss did not take in to account the above-ground biomass removed, hence the impacts on carbon sequestration and storage is far reaching.

Therefore, to minimize negative impacts under a mangrove forestry regime, fast recruitment of new trees, either by natural means or replanting, should be incorporated into the management plans, and areas of the forest exposed to wave energy should not be clearcut. Other ways of reducing pressures on mangrove forests should be explored; for instance, securing alternative sources of wood through afforestation with fast growing tree species in terrestrial sites.

CHAPTER THREE: THE IMPACTS OF CANOPY REMOVAL ON REGENERATION AND MACROFAUNAL ASSEMBLAGES IN A MANGROVE FOREST AT GAZI BAY, KENYA

Abstract

Through the modification of micro-habitat factors, mangrove plants strongly influence the biotic attributes within the mangrove ecosystem. Therefore, deforestation and degradation of mangroves may drastically impair biotic interactions in the system. This study assessed the impacts of tree canopy removal on vegetation recruitment and on the composition and abundance of macrofauna. The results showed that opening of the canopy, but retaining contiguous sources of propagules, enhanced regeneration. However, complete removal of all vegetation, including established saplings, impacted adversely on natural regeneration. However, seedling recruitment near the edges of cut plots was evident, suggesting that seedlings of *R. mucronata* follow the self-planting strategy rather than the stranding theory. Gap-preferring brachyuran crabs e.g. *Uca annulipes* (H. Milne Edwards, 1852) were observed to colonize open areas created by tree removal. On the other hand, the opening up of the canopy led to the decline of the gastropod species *Cerithidea decollata*.

3.1.   Introduction

Mangroves are regarded as biologically important areas that provide important ecological functions (Ewel *et al.*, 1998a). Adult mangrove plants have strong influence on benthic community structure and functions as well as plant recruitment and successional patterns (Macintosh *et al.*, 2002). Ecological interactions in mangrove ecosystems include the effects of plants as sediment modifiers, as sources of food for a range of benthic fauna and as structural support (habitat functions, coastal stabilization and runoff filtration) (Ewel *et al.*, 1998a; Alongi *et al.*, 2000; Alfaro *et al.*, 2006). Factors that influence the shaping of these ecosystem-based processes are complex and poorly understood. Furthermore, this is complicated by the natural and anthropogenic disturbances, which increasingly subject the mangroves to a lot of stress (Ferwerda *et al.*, 2007).

Habitat modification by human activities in mangrove ecosystems has been shown to affect abundance and diversity of benthic communities (Skilleter and Warren, 2000). Human disturbances in mangroves range from selective logging to total clearance (Ferwerda *et al.*, 2007). Mangrove forests are logged for wood products and cleared for activities such as aquaculture, the building of infrastructure and the construction of saltworks (Ferwerda *et al.*, 2007; Alongi and de Carvalho, 2008). It is estimated that over a third of mangrove forest globally has been lost due to human activities in the last 50 years (Valiela *et al.*, 2001). The major drivers of mangrove loss are over-exploitation and land use change (conversion of mangrove areas to other uses). Kenyan mangrove forests, which cover ~ 46 000 ha (Kirui *et al.*, 2012), have been subjected to degradation arising from over-

exploitation because of wood demand, especially for construction poles (Dahdouh-Guebas *et al.*, 2000; 2004). Since no management plans are in place for mangrove utilization, there is widespread degradation of the mangrove forests.

The ecological impacts of deforestation are complex because canopy removal can trigger a chain of events resulting in alteration of environmental conditions and changes in floral and faunal composition (Ewel *et al.*, 1998b; Sherman *et al.*, 2000). The dominant macrofauna in mangrove ecosystems in terms of species and numbers are the crustaceans and molluscs (Sasekumar, 1974; Macintosh *et al.*, 2002), hence they play an important role in the ecological functioning of mangrove ecosystems, e.g. as an important ecological link between mangrove detritus at the base of food web and the consumers at higher trophic levels (Macintosh *et al.*, 2002), and as modifiers of the mangrove's physical and vegetation structure through burrowing and foraging activities (Robertson and Daniel, 1989; Smith III *et al.*, 1991). Therefore, the impact of deforestation and degradation on macrofauna could have far reaching effects on ecosystem functioning (Fondo and Martens, 1998). The impacts of large-scale deforestation of mangroves on faunal abundance and diversity, and floral recruitment have been well documented (e.g. Baldwin *et al.*, 2001). However, the effects of small scale cutting by local communities for wood products on these aspects have been almost ignored (Alongi and de Carvalho, 2008); in particular there is a dearth of studies using replicated controlled methods, rather than opportunistic surveys, to study the effects of tree removal. Similarly, there is a paucity of information on the effects of disturbances on mangrove biotic attributes in the Western Indian Ocean region.

Vegetation recruitment, commonly referred to as natural regeneration, in mangrove forests has been largely quantified using linear regeneration sampling (LRS) (Sukardjo, 1987; FAO, 1994). In this technique, natural regeneration is usually assigned to three regeneration classes (RC) based size and/or age: RCI refers to seedlings of less than 30 cm height, RCII are seedlings/saplings of height up to 150 cm and RCIII are saplings of over 150 cm height but not mature enough for exploitation (FAO, 1994). However, the criteria for classification can be adjusted to suit local settings, since different sizes of mangrove stems are extracted for different purposes, which may warrant variations in size threshold for exploitation (FAO, 1994).

A number of census techniques have been used in assessment of the abundance and diversity of macrofaunal communities in mangrove ecosystems (Skov and Hartnoll, 2001; Skov *et al.*, 2002), notable among them include: pitfall trapping (Frusher *et al.*, 1994), mark–release–recapture (Hockett and Kritzler, 1972), counting burrow openings (Mouton and Felder, 1996), and counting crabs that are active on the surface (visual quantification) (Golley *et al.*, 1962). The adequacy, suitability and limitations of each of these techniques have been reviewed by Skov *et al*. (2002). Pitfall trapping has been shown to be selective by crab species and sex as well as requiring a number of days to be completed. Mark-release-recapture can only be applied to free roaming or migratory species and is also selective as it relies of capture of crabs. Visual observations and burrow counts were found to be the most suitable among the four techniques. However, visual observation was shown

to give an underestimation for crab species since it relies on the activities of the animals. On the other hand, burrow counts can lead to both under- and overestimation; underestimation results from some of the burrows being plugged off depending on tidal conditions. Likewise this technique is biased against non-burrowing species. On the other hand, overestimation occurs in situation where one individual utilizes more than one burrow (Skov *et al*., 2002). For gastropods visual observation in forest floor is biased towards those species which occupy the lowest strata in the vertical zonation and may underestimate species such as *Littoria sp* which are found mostly in the tree canopies (Richmond, 2011).

This study, therefore, aimed to evaluate the effects of canopy removal on:

a) The patterns and composition of sapling regeneration

b) The species composition and abundance of macrofauna in a mangrove forest at Gazi bay, Kenya.

3.2 Materials and Methods

3.2.1 Study Site

The study was carried out at Gazi bay (4^o25'S and 4^0 27' S; 39^o50'E and 39^0 50' E), ~ 55 km south of Mombasa, Kenya. Gazi bay is a coastal creek system with a total area of 615 ha mangrove forest (UNEP, 2001), dominated by *Rhizophora mucronata* (Lam)*, Ceriops tagal* (Perr.) C. B. Robinson and *Avicennia marina* (Forsk.) Vierh.

3.2.2   Experimental Design

The study was carried out in the same plots used for C fluxes and surface elevation experiment (Materials and Methods, Chapter 2). Observations were made during the baseline (March 2009 to October 2009), girdled (November 2009 to May 2010) and cut (May 2010 to April 2011) periods. All the seedlings and saplings < 1.5 m in height were removed during girdling and cutting treatments.

a)   Natural vegetation recruitment

LRS was used in the present study to assess the composition and densities of seedlings and saplings. Because, mangrove poles as small as 3 cm stem diameter have been show to be extracted in Kenyan mangrove forests (Dahdouh-Guebas *et al.*, 2000), 2.5 cm DBH was set as the smallest pole exploitable size. Therefore, the RCs were adjusted as follows: RCI (≤ 40 cm), RCII (40-150 cm), RCIII (1.5-3.0 m; diameter < 2.5 cm). Within each plot the species and abundance of all seedlings and saplings were recorded and grouped into three RCs set. Sampling was carried out in Match 2009, April 2010 and August 2011 during the baseline, girdled and cut periods, respectively.

b)   Macrofaunal abundance and composition

Within each plot, a 2 x 2 m^2 quadrat was set at the centre and permanent markers were placed at the corners. The abundance and composition of macrofauna were assessed by visual observations with the aid of binoculars within the quadrats. At least 20 minutes of observations were made in each plot at low tide and the total number of crabs per species

and family seen during the 20 minutes time of observation was recorded. Burrow counts, irrespective of species, were made in a 1 x 1-m^2 sub-set of the quadrat. Baseline sampling was done in September 2009 and subsequent counts were made in September 2010 and March 2011 (120 and 310 days after cutting, respectively).

3.2.3 Data Analysis

Because *R. mucronata* dominated the natural regeneration with other species were sparsely present, data analyses were performed for only *R. mucronata* using the MINITAB 14 software. The effect of treatment on the abundance of *R. mucronata* juveniles during the girdled and cut periods was tested using two-sample t-test and Mann-Witney test, respectively. The data during the cut period did not satisfy the assumptions of normality and homogeneity of variances even after various transformations were applied, and hence the use of non-parametric technique. The effect of distance from the plot edge on juvenile densities in the cut plots was tested using Mood's median test.

The crab species present in the plots were grouped by their respective families and the data were log-transformed and analysed using the MINITAB 14.0 software. The effect of treatment on the crab families was tested using a 3-factor nested ANOVA design, with the treatment nested in period and family nested in treatment. Similarly, the data for gastropod species was log-transformed and analysed using a 3-factor nested ANOVA design, in which the treatment was nested in period and species was nested in treatment.

Other biotic attributes of macrofauna community structure were analysed using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package (Clarke and Warwick, 1994). Biotic data similarity matrices were constructed using the Bray–Curtis similarity measure on non-standardized log-transformed data. The sample relationships from the similarity matrices were displayed using non-metric multi-dimensional scaling (MDS) (Kruskal and Wish, 1978; Clarke and Green, 1988; Warwick and Clarke, 1993). Significance tests for differences between treatments were performed using the analysis of similarity (ANOSIM) permutation test on the similarity matrices (Clarke and Green, 1988; Clarke, 1993). The species contributing most to the dissimilarities between treatments were investigated using the similarities percentage procedure (SIMPER; Clarke, 1993).

3.3 Results

3.3.1 Composition and Patterns of Natural Regeneration

Table 3.1. Composition and abundance of natural regeneration before and after treatment in *R. mucronata* forest at Gazi bay, Kenya; values are means ± standard errors: *Bg = B. gymnorrhiza, Ct = C. tagal, Rm = R. mucronata* and *Xg = X. granatum*

Period	Treatment	Species	Regeneration (saplings ha^{-1})			†Sprouts (RCI)
			RCI	RCII	RCIII	
Baseline		*Bg*	7±7	7±7	0	
		Ct	569±302	465±199	215±115	
		Rm	11750±1517	6451±867	2861±529	
		Xg	83±57	174±89	7±7	
Girdled	Control	*Ct*	236±155	97±97	97±81	
	Control	*Rm*	5833±1360	4500±1502	3986±1421	
	Control	*Xg*	0	17±16	0	
	Girdled	*Ct*	1153±642	0	0	
	Girdled	*Rm*	11167±1657	111±95	0	2000±384
	Girdled	*Xg*	56±34	0	0	
Cut	Control	*Ct*	14±14	0	56±56	
	Control	*Rm*	7194±464	7708±1410	4903±1648	
	Control	*Xg*	0	14±14	0	
	Cut	*Ct*	56±34	0	0	
	Cut	*Rm*	167±71	97±97	0	
	Cut	*Xg*	0	0	0	

†Saplings which sprouted after they were cut when the adult trees were girdled

Four species, in order of dominance, were encountered in the baseline sampling; *Rhizophora mucronata, Ceriops tagal, Xylocarpus granatum* and *Bruguiera gymnorrhiza* (Table 3.1). During both treatment periods, three species were encountered: *R. mucronata, C. tagal* and *X. granatum*, in order of dominance. There was a significant number of sprouts of saplings that were cut when the trees were being girdled (Table 3.1). During the

girdled period, treated plots registered a significantly higher regeneration than the controls (two sample t-test, t = -2.96, P = 0.02); whilst during the cut period, regeneration in the treated plots significantly declined (Mann-Whitney test, w = 15.0, P = 0.012). There was a significant effect of distance from the edge of the plot on the juvenile densities in the cut plots (Mood's median test; $\chi^2 = 7.6$, DF = 2, P = 0.02).

3.3.2 Macrofauna Composition and Abundance

Before treatment, seven brachyuran crab species belonging to two families were represented: the Sesarmidae [*Perisesarma guttatum* (A. Milne Edwards, 1869), *P. samawati* (Gillikin & Schubart, 2004), *Parasesarma leptosoma* (Hilgendorf, 1896), and *Neosarmatium smithii* (H. Milne Edwards, 1853)] and the Ocypodidae [*Uca chlorophthalmus* (H. Milne Edwards, 1837), *U. urvillei* (H. Milne Edwards, 1852), and *U. annulipes* (H. Milne Edwards, 1852)] (Figure 3.1a). During the baseline period *P. guttatum* was the dominant species, followed by *U. chlorophthalmus*. After the treatments were applied, *U. annulipes* dominated the treated plots, while *P. guttatum* was the dominant species in the controls. The sesarmids significantly dominated during the baseline period; whilst the ocypodids were significantly dominant in the treated plots (Figure 3.1a; nested ANOVA, P < 0.001). The patterns of crab burrow densities were similar for the baseline, control and cut plots (Figure 3.1b).
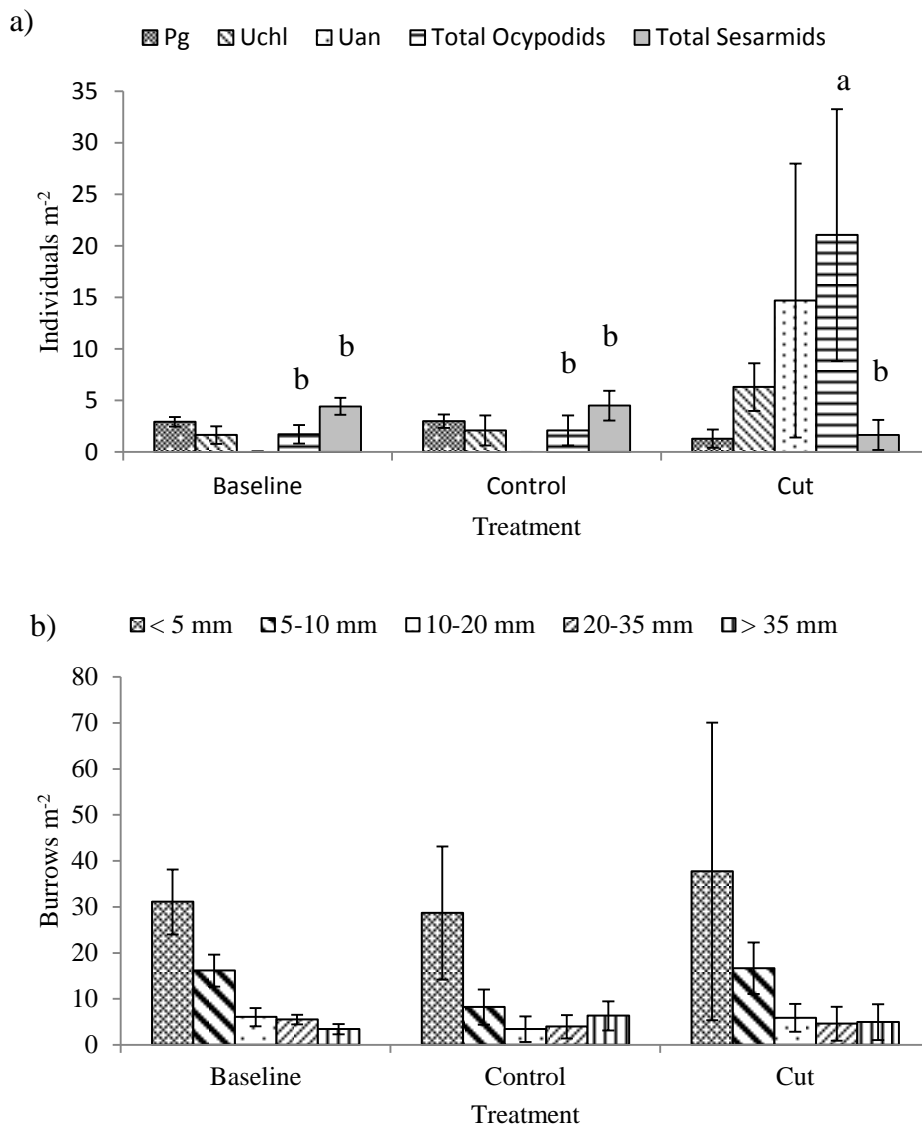
Figure 3.1 (a) Composition and abundance of brachyuran crabs and (b) crab burrow density before and after treatment in *R. mucronata* forest at Gazi bay, Kenya; Values are means ± 95% CI. Pg = *P. guttatum*, Uch = *U. chlorophthalmus* and Uan = *U. annulipes*: less abundance species in both treatments were omitted for clarity. Different letters above

bars indicate significant difference at α = 0.05; comparisons were made for crab families only.

Three gastropod species were encountered, with *Cerithidea decollata* being dominant during baseline sampling, followed by *Littoraria sp*, whilst *Melampus sp* was the least dominant (Figure 3.1b). Treatment significantly reduced the abundance of *C. decollata* (Figure 3.2; nested ANOVA, P < 0.01). There was no effect of treatment on *Littoraria sp* and *Melampus sp* (nested ANOVA, P > 0.325 and 0.286, respectively).

b
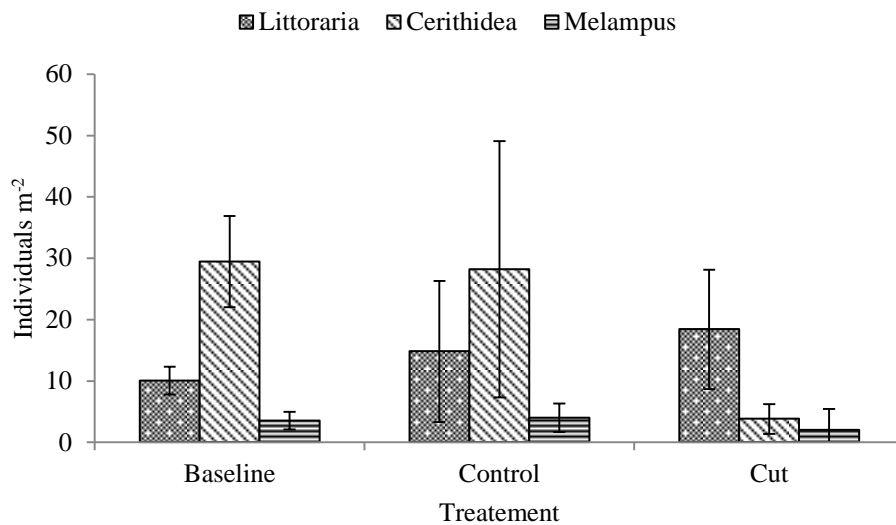
Figure 3.2. Composition and abundance of gastropods before and after treatment in *R. mucronata* forest at Gazi bay, Kenya; Values are means ± 95% CI. Different letters above bars indicate significant difference at α = 0.05.

The cut plots appeared to separate from the control plots in terms of macrofaunal community structure (Figure 3.2). One-way ANOSIM results supported this discrimination (Global R = 0. 645, P < 0.01), with the cut plots differing significantly from the baseline (P = 0.001) and control plots after treatment (P = 0.008). The SIMPER analysis showed that the treated plots were at least 44.1 and 41.7% dissimilar from the baseline and controls, respectively. *Uca annulipes* contributed most of these variations (29.3 % between cut and baseline, and 29.7 % between cut and controls); while *C. decollata* contributed secondly to the dissimilarity (16.0 % between baseline period and treated plots and 19.6 % between controls and treated plots).
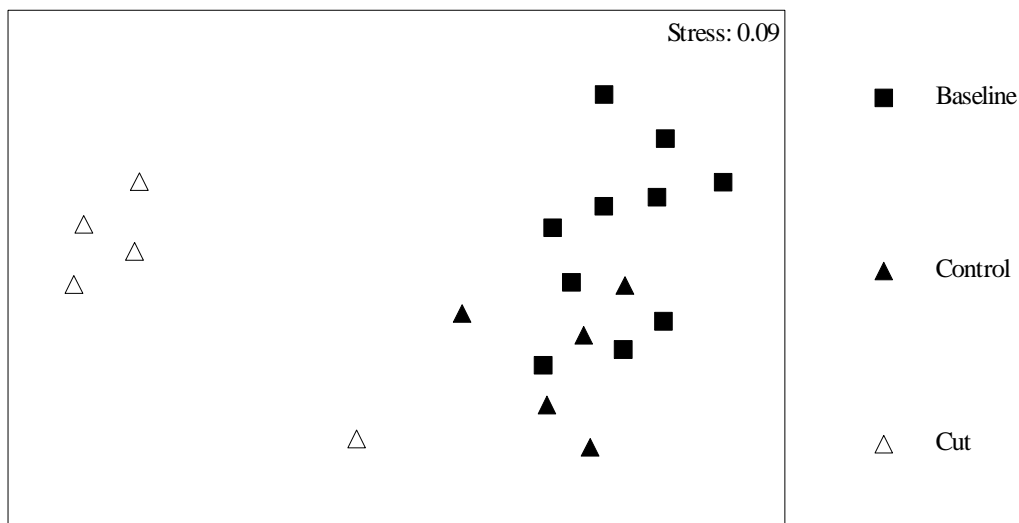
Figure 3.3. Non-metric MDS plots of baseline (closed squares), controls (closed triangles) and cut (open triangles) based on macrofauna species abundance in *R. mucronata* forest at Gazi bay, Kenya.

3.4 Discussion

3.4.1 Composition and Patterns of Natural Regeneration

Most mangrove forests in Kenya are not pristine (Kairo *et al.*, 2002) and the Gazi mangroves are no exception (Bosire *et al.*, 2003). As the only natural forests under concession in Kenya, they are subjected to intensive wood extraction, ranging from selective logging for poles and clear-cutting for fuelwood, especially for chalk making. As a result the logged areas are left degraded, while the clear-cut areas are denuded of mangrove trees with limited regeneration (Dahdouh-Guebas *et al.*, 2004). Natural regeneration in mangrove forests is a significant attribute in restocking the forest (Bosire *et al.*, 2008) and therefore, its impairment is detrimental to the future sustainability of the forests. Limited studies have been done on the effects of small-scale cutting in mangrove forests (Blanchard and Prado, 1995; Sherman *et al.*, 2000; Ferwerda *et al.*, 2007). Most of the studies on the effects of deforestation have been based on the disturbances by natural phenomena such as hurricanes (Roth, 1992; Baldwin *et al.*, 2001; Sherman *et al.*, 2001; Ferwerda *et al.*, 2007; McKee *et al.*, 2007c).

The girdled plots in the present study experienced high regeneration immediately after girdling. This was likely due to opening of the canopy occasioned by shedding of leaves of the girdled trees, thereby increasing light penetration. The girdled trees started shedding leaves three months after treatment and by the fourth month, most of the trees were leafless. This was similar to the robust regeneration observed in the hurricane damaged mangrove forests (Roth, 1992; Baldwin *et al.*, 2001). On the other hand, the cut treatment in this study

drastically impaired natural regeneration potential. All the seedlings and saplings were removed in the cut plots when the adult trees were cut. The removal of all vegetation was to avoid the effects of new roots on gas flux sampling, which was another on-going activity of the tree removal experiment. Therefore, the clearing of all seedlings and saplings during the cutting treatment might have contributed a significant experimental uncertainty to these results observed here, because during the conventional pole harvesting seedlings are normally left intact.

The sparse regeneration in the cut plots was most likely due to removal of seed trees that could supply propagules. Blanchard and Prado (1995) found that the absence of seed trees significantly influence the local availability of propagules in a given microsite. Consequently, the distance from plot edge or seed trees would also influence recruitment (Blanchard and Prado, 1995; McKee, 1995b). An analysis of juvenile densities with regard to distance from the plot edge in the cut plots in this study confirmed the fact that the proximity of seed trees significantly influence recruitment (Mood's median test; $\chi^2 = 7.6$, DF = 2, P = 0.02). It is therefore, evident from these results that propagule establishment was more likely to follow the 'self-planting' strategy, which favours their establishment under the parental tree (Dawes, 1980; Tomlinson, 1986). This was contrary to the findings from an earlier study at Gazi (Van Speybroeck, 1992), which indicated that the 'stranding' strategy was superior over the 'self-planting' strategy in over-exploited mangroves than in un-disturbed sites. A number of authorities have provided evidence for both the 'stranding' (Rabinowitz, 1978; Tomlinson, 1986) and 'self-planting' theories of propagule

establishment (Dawes, 1980; Tomlinson, 1986). Under the 'stranding' theory, mangrove propagules are washed away by tides and get established in sites with favourable conditions, but away from parental trees. On the other hand, the 'self-planting' theory stipulates that the propagules are pointed to facilitate establishment under the parental canopy. So the evidence here supports the establishment of propagules within the proximity of the parental canopy, whose removal can adversely impact the juvenile recruitment.

3.4.2 Composition and Abundance of Macrofauna

The distribution of some mangrove macrofaunal species are affected by mangrove canopy shade, which influence light penetration, temperature fluctuations and soil moisture content (Nobbs, 2003; Kon *et al.*, 2010). Loss of canopy cover in mangrove forests leads to modification in sediment characteristics, which would in turn influence the species composition of benthic communities. There were highly significant changes in community structure following canopy clearance in the present study. The removal of tree canopy in the treated plots favoured the abundance of gap-preferring macrofaunal species, particularly, *U. annulipes*; this trend was similar to that observed for the same species in Thailand (Kon *et al.*, 2010). Dietary habit has been found to be one of the most important factors that influence habitat preference by brachyuran crabs (Machiwa and Hallberg, 1995). Therefore, open canopies, which enhance the production of algal materials, are preferred by most of the deposit feeders such as *U. annuilpes* (Machiwa and Hallberg, 1995; Kon *et al.*, 2010). The burrow counts did not show any variations between the control and the cut plots. Although the burrow count technique can give an estimate of crab

abundance at the family level (Skov *et al.*, 2002), it is difficult to discriminate the composition of crabs to species level.

Cerithidea decollata abundance reduced significantly in the treated plots. This species has been observed to utilize biotic structures such as tree stems for climbing during high tide (Machiwa and Hallberg, 1995; Richmond, 2011). However, since tree stumps with stilt roots up to 1 m height were left behind in the treated plots, the most plausible explanation is that this gastropod species prefers shaded sites. The con-generic species, *C. cingulata* was observed to increase in shaded areas in Thailand (Kon *et al.*, 2010). Since all *Littoraria* species are mostly found in the tree canopies (e.g. Richmond, 2011), the results presented here may be an underestimation of individuals of this genus.

3.5 Conclusions

A number of ecological interactions exist between the biotic attributes in mangrove ecosystems. The vegetation provides a number of ecological functions to benthic communities, which include habitat functions, refuge from predators as well as source of food. The benthic communities on the other hand play important roles in processes such as nutrient cycling as well as sediment aeration. However, habitat modifications even from small-scale disturbances threaten to impair these important interactions.

The opening of the tree canopy through loss of leaves, but with the continuing presence of seed trees can lead to robust regeneration. This was confirmed by the high regeneration

observed immediately after girdling. Girdling led to loss of leaves four months after treatment, but ensured sufficient light penetration for seedling recruitment. However, this study has also confirmed that removal of seed trees coupled with destruction or damage of established regeneration can drastically impair seedling recruitment. Similarly, these results have emphasised the importance of availability of sufficient seed trees for good regeneration. It was found that *R. mucronata* seedlings favoured the 'self-planting' strategy over the 'stranding' strategy, at least over the time scales considered here. However, the sparse regeneration observed in the cut plots cutting in this study was exacerbated by the clearing of all seedlings and saplings for the gas flux experiment being conducted in the same plots.

These results also showed that removal of tree canopy led to a shift in the dominance of macrofauna species. Gap-preferring brachyuran crabs such as *U. annulipes* colonized and dominated cut plots; this was likely driven by enhanced algal productivity induced by ample light penetration in open areas. On the other hand gastropod species such as *C. decollata* were adversely impacted by canopy opening. The loss of shade with the cool micro-environment that it allows might have been responsible for the decline of this gastropod species. Therefore, these findings have confirmed that small-scale cutting can result in significant effects on community characteristics in mangrove ecosystems.

CHAPTER FOUR: MANGROVE FOREST PRODUCTIVITY PATTERNS

ACROSS INTERTIDAL GRADIENT

Abstract

Patterns of allocation of new biomass by plants are constrained by environmental stressors that limit resource availability. Mangrove plants grow in unstable, hypoxic and nutrient-poor soils, and hence they tend to invest more in belowground growth than terrestrial trees, in order to maximize resource acquisition under anaerobic conditions. However, due to the methodological difficulties in estimating belowground productivity of mangroves, there is limited information on the determinants of root growth in mangroves. The present study aimed at estimating belowground production and below- to aboveground productivity patterns in mangrove forests at Gazi bay, Kenya. *Rhizophora mucronata* invested more in aboveground biomass (AGB) production (mean root:shoot ratio = 0.20), while *Avicennia marina* allocated more biomass to belowground root (BGB) production (mean root:shoot ratios of 1.25). *Ceriops tagal* had the highest proportion of fine root (< 3mm) production. High porewater salinity tended to lead to low investment in AGB production, while low soil moisture and high redox potential significantly enhanced BGB production. This study has shown that mangrove plants at least invest more carbon in root growth as an adaptive mechanism against environmental stressors. Secondly, it has been shown that there exists a relationship between above- and belowground biomass in mangroves forests.

4.1   Introduction

The ratio of biomass allocated to different parts of a plant, in particular to the root vs the shoot system, reflects a key adaptive response that varies within and between species and depends of a large range of environmental factors. Plants in nutrient poor soils tend to allocate proportionately more biomass to the root system in order to acquire the most limiting resources (Chapin III *et al.*, 1987; Gleeson and Tilman, 1992; Castaneda-Moya *et al.*, 2011). Vegetated wetland ecosystems such as mangroves are faced with a daunting range of environmental stressors such as nutrient deficiency, hypoxia and hydroperiodism (Feller *et al.*, 2003a; Twilley and Rivera-Monroy, 2005; Lin *et al.*, 2010). Mangrove plants are adapted to these dynamic environmental conditions through a number of morphological and physiological mechanisms (e.g. Feller *et al.*, 2003a; 2003b), including a high investment in belowground roots, with up to 40-60 % of biomass allocated to roots. Hence mangrove plants generally have higher root:shoot ratios than their terrestrial counterparts (Golley *et al.*, 1962; Briggs, 1977; Lugo, 1990; Komiyama *et al.*, 2000; 2008).

High allocation of carbon to belowground roots in mangroves has implications for the ecological functioning of mangrove forests. The sediment organic matter input and root exudates resulting from this process ensures availability of C to detritivores and other consumers. In addition, high rates of organic deposition by the trees, coupled with low decomposition rates of plant material in the anoxic mangrove sediments (Middleton and McKee, 2001) and the trapping of allochthonous sediments, contribute to surface elevation, thus helping mangroves keep pace with sea level rise (Cahoon and Lynch, 1997; McKee *et al.*, 2007). These processes of root production, slow decomposition and sediment trapping

can result in the accumulation of very large and persistent carbon stocks in mangrove soils. Mangroves thus play an important part in regional carbon cycles and contribute to climate change mitigation (Twilley *et al.*, 1992; Fujimoto *et al.*, 1999; Bouillon *et al.*, 2008; Kristensen *et al.*, 2008a; Castaneda-Moya *et al.*, 2011; Donato *et al.*, 2011).

The major carbon input to the mangrove system is through autochthonous plant productivity. The methods commonly used in estimation of primary productivity of mangrove forests include: litter fall, harvesting, gas exchange, light attenuation and demographic/allometric changes (Along, 2009). The most widely used proxy for mangrove productivity is annual litter fall (e.g. Twilley *et al.*, 1992; Jennerjahn and Ittekkot, 2002) because it is cost effective and easy to measure, however, this is an underestimate since it does not incorporate wood and root production and dissolved organic carbon (DOC) released through root exudates (Kristensen *et al.*, 2008). Harvesting is labour intensive and slow, as well as available only as a result of silviculture. In addition, like litter fall, it only accounts for aboveground production, albeit, with leaf production unaccounted for. Gas exchange measurements (e.g. Clough and Sim, 1989) are precise and rapid, but subject to problems of extrapolating from a small area to the whole stand. In addition, it overestimates net production since does not account for most of tree respiration. Light attenuation (Clough *et al.*, 1997) offers the best method of measuring primary productivity of mangroves, but it relies on the measurement of light absorption and the average rate of photosynthesis per unit leaf area should be measured at each site (Alongi, 2009). Monitoring of demographic changes and incremental growth (Komiyama *et al.*, 2008) is easy to undertake, but relies on allometric relationships, which are often site and species-

specific, to convert incremental growth to production based on carbon allocation (Alongi, 2009).

Globally, net primary productivity (NPP) of mangroves is estimated to be ~149 mol C m^{-2} year^{-2}; with litter fall, above-ground wood and root production representing ~ 38, 67 and 44 mol C m^{-2} year^{-2}, respectively (Twilley *et al.*, 1992; Jennerjahn and Ittekkot, 2002). This indicates that contribution of litter fall to NPP ranges from 10-25% (Alongi *et al.*, 2005; Kristensen *et al.*, 2008a); while belowground root production makes a substantial part (10-55%) of plant biomass (Saenger, 1982; Twilley *et al.*, 1992; Matsui, 1998; Alongi and Dixon, 2000; Sánchez, 2005).

Copious information is available on aboveground primary production in mangrove forests (e.g. Ross *et al.*, 2001; Sherman *et al.*, 2003; Komiyama *et al.*, 2008). Whilst there is a growing body of information of below-ground biomass and necromass in mangrove forests (see for e.g. Tamooh *et al.*, 2008) technical difficulties mean that estimates of belowground productivity remain rare (McKee and Faulkner, 2000; Gleason and Ewel, 2002; Sánchez, 2005; McKee *et al.*, 2007a; Castaneda-Moya *et al.*, 2011; McKee, 2011). Hence there remains little information on below-ground productivity and what controls it in mangroves, despite its crucial ecological importance in these forests. The opportunity to market mangrove carbon, most of which is stored below-ground, in emerging global carbon markets as a way of funding mangrove conservation raises an important applied argument for better understanding of below-ground dynamics in these forests. Whilst understanding the relationship between above and below-ground productivity is of interest in itself it

could also allow simpler and cheaper estimates of below-ground processes to be made (if, for example, predictive relationships were established that allowed above-ground measurements to act as accurate proxies). The present study, therefore, aimed to a) determine root productivity in four mangrove species and explore the effects of environmental conditions on root production and b) determine the below- to aboveground productivity patterns in mangrove forests in Gazi bay, south coast of Kenya.

4.2   Materials and Methods

4.2.1   Study site

The study was carried out at Gazi bay (4^o25'S and 4^0 27' S; 39^o50'E and 39^0 50' E), ~ 55 km south of Mombasa, Kenya (Figure 1.2, Chapter One). Gazi bay is a coastal creek system with a total area of 615 ha mangrove forest (UNEP, 2001), dominated by *Rhizophora mucronata* (Lam)*, Ceriops tagal* (Perr.) C. B. Robinson and *Avicennia marina* (Forsk.) Vierh*. Sonneratia alba* (J. E. Smith) occupies the seaward front, acting in most sites as a pioneer species in seaward accreting mud. The environmental attributes of the selected forest types at the start of monitoring are shown in Table 4.1.

4.2.2   Experimental design

Twenty eight 10 m x 10 m plots were established in four mangrove forest types, *Rhizophora mucronata, Ceriops tagal, Sonneratia alba* and *Avicennia marina,* situated in two sites. Ten of the plots were established in Makongeni (five replicates each in *R. mucronata* and *A. marina* forest) in September 2009, while 18 plots were established in

Gazi comprising of all the four mangrove forest types in July 2010; six replicates each in *R. mucronata* and *A. marina* forests and three replicates each in *C. tagal* and *S, alba* forests.

4.2.3   Vegetation and Environmental Attributes

Forest Structure

The aboveground structural attributes (stem diameter, tree height, stem density, basal area and the aboveground biomass) of the forest were described. For each tree (with ≥ 2.5 stem diameter) within each plot the stem diameter (DBH; diameter at breast height) was measured using a forester's calliper at 130 cm above the ground (Brokaw and Thompson, 2000) for *A. marina* and *S. alba* trees. The point of DBH measurement was adjusted for *C. tagal* trees (most trees of this species were < 3 m in height) and *R. mucronata* trees to be taken, respectively, at half the tree height and ~ 30 cm above the highest prop root. The tree height was measured using graduated pole, respectively. From this data, the stem density, basal area and aboveground biomass (AGB) were derived. Basal area (m^2) was calculated as: $BA = 0.00007854 DBH^2$ (Cintron and Schaeffer-Novelli, 1984), where DBH = stem diameter.

The AGB was derived from the mixed effects models (Gelman and Hill, 2007) developed for the mangrove forests of Gazi bay (R. Cohen in preparation). The aboveground tree datasets of stem diameter (≥ 2.5 cm) and tree height (≥ 2 m) for Gazi bay mangroves (Kirui *et al*., 2006; Kairo *et al*., 2008; Tamooh *et al.,* 2008; Lang'at et al., Unpublished) were used to develop the mixed effects models. Site-species-specific equations were developed for *R. mucronata* at Gazi and Makongeni sites since harvest datasets for this species at the two sites were available (Kirui *et al.*, 2006; Kairo *et al.*, 2008; Tamooh *et al.*,

2008); while a generic equation was developed for all other species mangrove species in which only the aboveground structural datasets but with no harvest datasets (R. Cohen in preparation):

LnAGB = -1.914872 + 1.77556*(lnDBH) + 0.9238012*(lnHt)+0.30916 (R. mucronata forest, Gazi),

LnAGB = -3.068174 + 1.77556*(lnDBH) + 1.2807482*(lnHt) +0.30916 (*R. mucronata* forest, Makongeni) and

LnAGB = -2.144857 + 1.77556*(lnDBH) + 0.62822*(lnHt) +0.30916 (other mangrove species at Gazi bay)

Where AGB = aboveground biomass, DBH = stem diameter and Ht = tree height.

Environmental Variables

Environmental variables such as height above sea-level and soil phyico-chemical characteristics (soil redox potential, porewater salinity and soil grain size) were assed at the initial experimental set up. The height above sea-level (m) for each plot was determined from measurement of height of the water column in the plots at high tide and subtracted from the high tide prediction for the day of measurement.

Each plot was divided in to four equal quarters and four surface scrapes, each at a random point in each quarter, were scooped to 1 cm depth using a 10-cm long 6 cm x 6 cm corer.

The subsamples for each plot were reconstituted as one sample, mixed well in labelled airtight plastic bags and taken to the laboratory for grain size analysis. In the laboratory the samples were weighed and oven-dried at 80° C for 24 hours after which they were weighed again to determine the soil moisture (SOM) content. Twenty five (25) grams oven-dry weight of each sample was treated with 10 ml of aqueous sodium hexametaphosphate $((NaPO_3)_6)$ in a labelled beaker and subjected to a series of sieves; ranging from 63 to 500 μm mesh-size, to determine the portion of different grain sizes (i.e., < 63, 63-500 and > 500 μm particle size).

Redox potential and salinity samples were obtained from four random points in each plot at 10 and 40 cm depth using a D-section soil corer. Redox potential measurements were made using a portable redox meter as soon as the core was removed. For salinity ~ 50 g of the samples were taken for centrifuging in the laboratory to extract pore water, which was tested for salinity using a handheld refractometer.

4.2.4   Above- and Belowground Productivity Monitoring

The aboveground productivity was estimated by applying the mixed effects models describe above (section 4.2.3) to the growth increment variables monitored within the plots. In each plot 10 trees were tagged based on size class distributions (in order to sample a representative range of trees in each plot) and a dendrometer was installed on one of the selected trees in each plot (hence the limited number of dendrometers were dispersed between all plots and used to validate the calliper measurements). Girth measurement of the tagged trees and the dendrometer reading were taken every three months.

Within each plot two in-growth trenches, 20 cm x 80 cm x 40 cm deep were dug out. Sediments together with roots were excavated from each trench. The roots were removed, macerated with a matchet in to small pieces, mixed with the sediment and the root fragment/sediment mix was then returned to the trench. Mangrove roots grow towards nutrient rich areas and away from nutrient poor ones, with old roots acting as nutrient stores (McKee, 2001). Hence it was important to use the ambient sediment without removing the roots that were present; macerating them enabled the separation of old roots from in-growth roots that might have died before retrieval. The positions of the trenches were marked with PVC pipes driven into the ground leaving ~ 5 cm projecting. The in-growth trenches in the Makongeni plots were recovered in July 2010 (330 days) and May 2011 (after 625 days), while those in Gazi plots were recovered between July and August 2011 (after 280 days). The in-growth materials were extracted in two depth profiles; 0-20 and 20-40 cm. The samples from each depth profile were washed of sediments and put in labelled plastic bags to be processed and analysed later in the laboratory. In the lab, the roots were sorted in to live and dead roots based on the structural integrity, colour and signs of decomposition (McKee *et al.*, 2007). Live roots were further sorted into fine (< 3 mm) and coarse ($\geq$ 3 mm) roots. All the samples of live roots were oven-dried at 80 $^{\circ}$C to constant weight. Dead roots were very scanty and hence were not included in analysis. Below-ground productivity for each plot was calculated as oven-dried weight of the samples divided by the time taken between set up and retrieval and expressed as dry-weight per unit area per year.
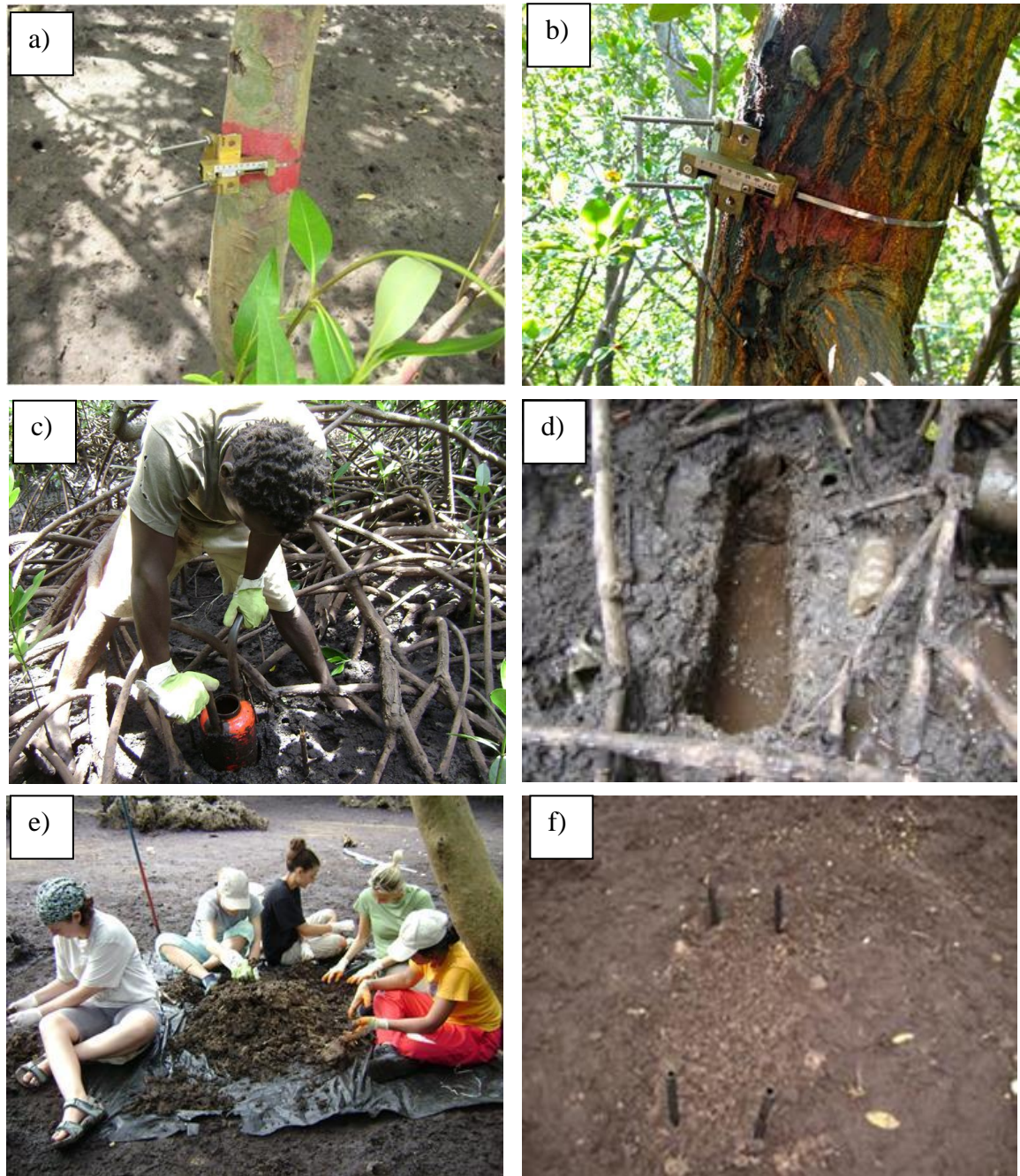
Plate 4.1. Mangrove growth increment monitoring set up; a) and b) dendrometers installed

in *A. marina* and *R. mucronata* trees, respectively, c) and d) preparation of an ingrowth

trench in *R. mucronata* forest, e) sorting of excavated roots to be macerated and returned to the ingrowth trench and f) a completed ingrowth trench with PVC pipes marking its dimensions in an *A. marina* plot.

4.2.5   Statistical Analysis

The values for AGB, BGB production and RSR_p were log-transformed and analysed using the MINITAB 14.0 software package. To test between forest sites and types a nested ANOVA approach was used with species nested in site. Pairwise comparisons were performed for the terms with significant differences. Multiple regressions (using forward, backward and stepwise methods) were performed with belowground root production as the dependent variable and AGB production and environmental variables as the independent variables. Variance inflation factors were used to test for colinearity, and factors found to be highly correlated were removed from the regressions. Similarly, multiple correlations were performed between the environmental variables (topographic height, porewater salinity, redox potential, grain size and soil moisture) and productivity variables.

4.3   Results

4.3.1   Vegetation and Environmental Attributes of the Forests

Forest Structure

Except for *C. tagal*, which represented a scrub forest, all the other forest types had fairly average-sized trees (Table 4.1). *Rhizophora mucronata* (in both sites) and *S. alba* forests exhibited high aboveground biomass.

Table 4.1. Stand table of four mangrove forest types at Gazi bay, Kenya: values are means ± 95%CI, G and M represent Gazi and Makongeni sites, respectively

Forest	Stand density (Stems ha^{-1})	DBH (cm)	Tree Ht (m)	Basal area (m^2 ha^{-1})	AGB (t ha^{-1})
A. marina (G)	4300 ± 884	6.2 ± 2.0	5.0 ± 1.4	15.2 ± 7.3	61.1 ± 34.6
A. marina (M)	3040 ± 314	6.8 ± 0.3	5.1 ± 0.3	14.5 ± 2.8	57.9 ± 10.8
C. tagal (G)	5133 ± 1840	3.2 ± 0.7	2.4 ± 0.4	5.9 ± 4.3	11.8 ± 4.7
R. mucronata (G)	4067 ± 474	5.3 ± 1.0	5.2 ± 0.4	13.6 ± 4.2	122.9 ± 42.8
R. mucronata (M)	4660 ± 671	5.4 ± 0.4	5.5 ± 0.3	17.2 ± 2.8	125.7 ± 32.6
S. alba (G)	3633 ± 285	8.7 ± 3.7	6.1 ± 1.9	27.1 ± 18.4	112.9 ± 80.8

Environmental Characteristics

The physico-chemical characteristics of the four forest types and the two sites are shown in Table 4.2. Most of the sediment characteristics of the forest types assessed were within the range observed for Gazi bay mangroves (e.g Gallin *et al*., 1989). However, the two sites exhibited slightly different sediment characteristics, with the Makongeni mangroves showing of lower porewater salinities, higher proportion of fine textured soils (< 63 μm) and less reduced sediments (particularly for *A. marina* forest) depicting a more favourable environment as compared to the Gazi site.

Table 4.2. Environmental variables measured from the different forest types and sites at Gazi bay, Kenya: values are mean ± 95% CI

Site	Variable		*Avicennia*	*Ceriops*	*Rhizophora*	*Sonneratia*
Gazi	Topographic height (m)		3.5±0.2	2.9±0.0	2.5±0.1	1.7±0.0
	Salinity (‰)	*10 cm*	39.3±7.9	35.0±4.1	30.0±2.9	29.5±4.0
		40 cm	42.0±14.2	36.7±6.9	28.3±1.2	30.5±0.8
	Redox (mV)	*10 cm*	129.6±18.2	-23.3±62.1	-32.5±55.9	-113.0±169.0
		40 cm	-57.7±33.7	-267.5±62.1	-79.1±124.7	-66.8±172.3
	Soil moisture (%)		28.3±6.2	55.9±7.4	47.3±4.4	24.4±5.0
	Grain size (%)	*< 63 μm*	20.4±8.0	68.9±5.9	52.7±9.6	14.0±9.0
		63-500 μm	63.7±15.3	24.4±10.9	36.7±5.6	65.9±13.5
		> 500 μm	15.9±7.5	6.7±7.9	10.6±4.4	20.1±4.5
Makongeni	Topographic height (m)		3.3±0.1		2.8±0.0	
	Salinity (‰)	*10 cm*	34.1±1.3		31.1±2.4	
		40 cm	32.0±3.3		32.7±1.9	
	Redox (mV)	*10 cm*	185.4±40.4		-43.4±52.9	
		40 cm	170.1±61.2		-148.0±87.4	
	Soil moisture (%)		34.8±7.6		46.9±8.4	
	Grain size (%)	*< 63 μm*	53.6±12.4		43.1±12.6	
		63-500 μm	31.9±10.5		33.3±7.1	
		> 500 μm	14.4±2.0		23.6±7.1	

4.3.2   Aboveground Biomass (AGB) Production

Table 4.3. Nested ANOVA of four mangrove types at Gazi bay, Kenya. AGB = aboveground biomass production, BGB = live belowground biomass production and RSR_p = root:shoot production ratios

Variable	Source	DF	MS	F	P
AGB	Site	1	0.99619	29.71	< 0.001
	Species (Site)	4	0.30133	8.99	< 0.001
	Error	22	0.03353		
BGB	Site	1	1.41331	35.46	< 0.001
	Species (Site)	4	0.33030	8.29	< 0.001
	Error	22	0.03985		
RSR_p	Site	1	0.03782	0.52	0.477
	Species (Site)	4	0.47631	6.58	0.001
	Error	22	0.07236		

The AGB production ranged from 200.0-677.1, 77.0-339.0, 540.0-2849.5 and 287.0-773.0 g m^{-2} yr^{-1} for *A. marina*, *C. tagal*, *R. mucronata* and *S. alba*, respectively. There was significant variation between the two sites, with Makongeni mangroves having higher AGB production than those of Gazi (Table 4.2). Makongeni *R. mucronata* forest (Rm-M) had significantly higher AGB increment compared to all other forest types (Figure 4.1a; P < 0.05).
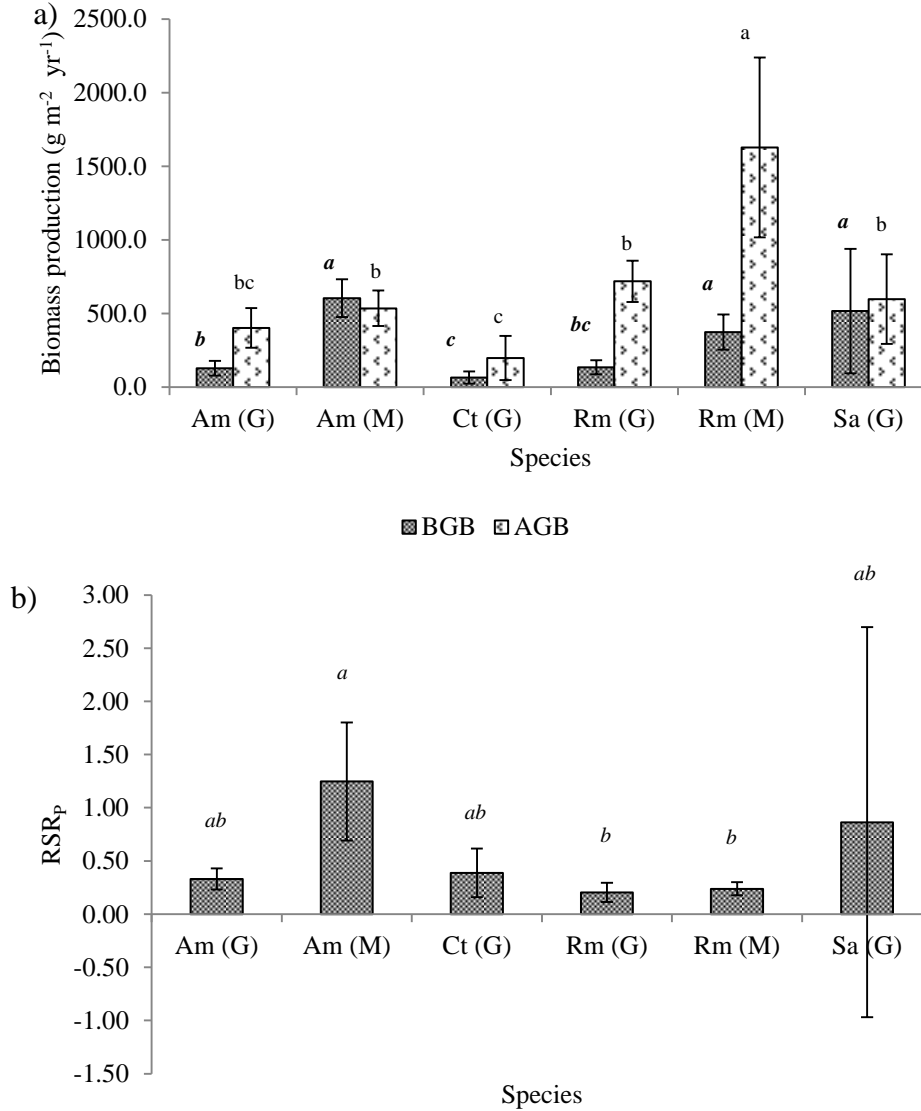
Figure 4.1. (A) Above- and belowground biomass production and (B) root-shoot production ratio (RSR$_p$) in mangrove forests of Gazi bay, Kenya. Error bars are 95% CI, AGB = aboveground biomass, BGB = belowground biomass, *Am = Avicennia marina*, *Ct = Ceriops tagal Rm = Rhizophora mucronata* and *Sa = Sonneratia alba*, G and M represent Gazi and Makongeni sites, respectively. Different letters above the bars for each component indicate significant variation at $\alpha = 0.05$.

Makongeni *A. marina* (Am-M), Gazi *R. mucronata* (Rm-G) and *S. alba* had significantly higher AGB production than *C. tagal* forest (Figure 4.1; $P < 0.05$). Among the environmental variables, only porewater salinity correlated significantly (and negatively) with AGB production (Table 4.3).

Table 4.4. Correlations between biomass production and environmental variables in mangrove forests of Gazi bay, Kenya

Variable		AGB		BGB		RSR_p	
		R	P	R	P	R	P
Topographic height (m)		-0.255	0.190	-0.040	0.840	0.173	0.377
Salinity (‰)	*10 cm*	-0.609	0.001	-0.218	0.285	0.303	0.132
	40 cm	-0.523	0.007	-0.205	0.327	0.241	0.246
Redox (mV)	*10 cm*	-0.271	0.163	0.449	0.016	0.520	0.005
	40 cm	0.043	0.823	0.651	0.000	0.597	0.001
Soil moisture (%)		0.065	0.744	-0.427	0.023	-0.470	0.012
Grain size (%)	*< 63 μm*	0.049	0.806	-0.254	0.192	-0.208	0.289
	63-500 μm	-0.053	0.789	0.114	0.563	0.156	0.429
	> 500 μm	0.274	0.153	0.437	0.020	0.198	0.313

4.3.2 Belowground Biomass (BGB) Production

Belowground root production ranged from 96.9-804.5, 30.3-102.5, 58.0-580.8 and 185.8-921.7 g m^{-2} yr^{-1} for *A. marina*, *C. tagal*, *R. mucronata* and *S. alba*, respectively. Makongeni mangroves had a higher root production than those of Gazi section (Table 4.2, $P = 0.005$). *Post hoc* analysis indicated the Makongeni *A. marina* had a significantly higher root production than Gazi *A. marina*, *C. tagal* and *R. mucronata*. Makongeni *R. mucronata* and *S. alba* had significantly higher live belowground biomass (BGB) production than *C. tagal* and Gazi *R. mucronata* (Figure 4.1; $P < 0.05$).

Coarse roots contributed most to root production in all the forests types except in *C. tagal*

forest (Table 4.4). Root production correlated significantly with soil moisture content (R = -

0.6, P < 0.05), redox potential (R = 0.8, P < 0.05) and the proportion of coarse soil particles

(R = 0.6, P = 0.02).

Table 4.5. Proportion (%) of fine (< 3 mm) and coarse (≥ 3 mm) root production in four

mangrove forest types at Gazi bay, Kenya

Species	Depth (cm)	Gazi		Makongeni	
		< 3 mm	≥ 3 mm	< 3 mm	≥ 3 mm
A. marina	0-20	26.6	73.4	16.3	83.7
	> 20	26.9	73.1	7.4	92.6
C. tagal	0-20	52.4	47.6	-	-
	> 20	77.3	22.7	-	-
R. mucronata	0-20	23.1	76.9	33.1	66.9
	> 20	21.3	78.7	27.4	72.6
S. alba	0-20	17.3	82.7	-	-
	> 20	12.6	87.4	-	-

The relationship between the AGB and BGB for each species was not significant (P > 0.05,

for all cases), hence the species-specific AGB-BGB relationships are not presented.

4.3.3   Root:Shoot Production Ratios (RSR$_p$)

The root:shoot production ratios ranged from 0.3-3.1, 0.2-0.6, 0.1-0.4 and 0.2-2.8 for *A.*

marina, *C. tagal*, *R. mucronata* and *S. alba*, respectively. RSR$_p$ did not vary significantly

between the two sites (Table 4.2). *Avicennia marina* at Makongeni had a significantly

higher RSR$_p$ than *R. mucronata* at the both sites (Figure 1; P < 0.01). Root:shoot

productivity ratios showed significant negative correlations with soil moisture ($R = -0.5$, $P < 0.01$) and significant positive ones with redox potential ($R = 0.6$, $P < 0.01$).

4.4   Discussion

4.4.1   Aboveground Biomass (AGB) Production

The aboveground biomass production values of the four mangrove forest types at Gazi bay were within the range reported for mangrove forests in other parts of the world (Table 4.6). for instance, *R. mucronata* at Makongeni had annual AGB production (16.28 t ha^{-1} yr^{-1}) similar to that of *R. appiculata* in Malaysia (12.38 t ha^{-1} yr^{-1}) (Ong *et al.*, 1995). *Avicennia marina* AGB production in both sites studied here was higher than that of *Avicennia* species in Sri Lanka (1.40 t ha^{-1} yr^{-1}) and Mexico (0.92-2.02 t ha^{-1} yr^{-1}) (Amarasinghe and Balasubramaniam, 1992; Day *et al.*, 1996).

Aboveground biomass production for Gazi bay mangroves varied significantly among the two sites and forest types. The mangroves of Makongeni had higher biomass production than those in proximity to Gazi village ($P < 0.001$). Spatial variation in forest productivity has been attributed to climate variability, site characteristics and site history (Ryan *et al.*, 1997; Sherman *et al.*, 2003). However, local variation in mangrove biomass production has been shown to be driven by local environmental stressors such as salinity, redox potential, nutrient availability and tidal inundation (Feller *et al.*, 2003a; 2003b; Sherman *et al.*, 2003). It is very likely that local environmental conditions might have contributed to the variation in the biomass increment between the two sites.

Table 4.6. Comparison of AGB production of mangrove forests of various places across the world

Forest Type/setting	Dominant species	Tree Ht (m)	Latitude	AGB (t ha^{-1} yr^{-1})	Country	Reference
Basin, landward	*Avicennia*	5.1	4.65	4.69	Kenya	This study
Scrub	*Ceriops*	2.4	4.65	1.97	Kenya	"
Basin, interior	*Rhizophora*	5.4	4.65	11.73	Kenya	"
Fringe	*Sonneratia*	6.1	4.65	5.97	Kenya	"
	Rhizophora	3.5	8.15	6.77	Sri Lanka	Amarasinghe and Balasubramaniam (1992)
	Rhizophora and *Avicennia*	3.5	8.15	5.62	Sri Lanka	"
	Rhizophora	3.5	8.15	4.33	Sri Lanka	"
	Avicennia	3.5	8.15	1.40	Sri Lanka	"
	Rhizophora and *Avicennia*	6	18.40	1.99	Mexico	Day *et al*. (1996)
	Avicennia	4	18.40	0.92	Mexico	"
	Avicennia	6	18.40	2.02	Mexico	"
	Rhizophora	11	8.00	20.00	Thailand	Christensen (1978)
	Rhizophora	21	4.50	12.38	Malaysia	Ong *et al*. (1995)
	Rhizophora	8.6	18.00	3.07	Puerto Rico	Golley *et al*. (1962)
	Avicennia	20	18.40	12.06	Mexico	Day *et al*. (1987)
	Rhizophora	6	18.40	7.72	Mexico	"

Even though most of the sediment characteristics of the forest types assessed were within the range observed for Gazi bay mangroves (e.g Gallin *et al*., 1989), the two sites exhibited slightly different sediment characteristics, with the Makongeni mangroves showing of lower porewater salinities, higher proportion of fine textured soils (< 63 μm) and less reduced sediments (particularly for *A. marina* forest) depicting a more favourable environment with less stressors as compared to the Gazi site. In addition the two sites have slightly different geomorphological settings. The mangroves to the west of Kidogoweni creek, comprising the Gazi mangroves, have narrow intertidal width, while those to the east, which include Makongeni forests, have a wide tidal width (Fig 1.2, Chapter 1). A larger intertidal area encourages robust growth of mangrove plants (Kathiresan and Qasim, 2005). Salinity negatively influenced AGB production (Table 4.4), which concurs well with the evidence that increasing salinity negatively affects structure and productivity of mangroves (Ball, 1988; Sherman *et al.*, 2003; Lovelock *et al.*, 2004; Naidoo, 2006) by affecting physiological processes such as photosynthetic performance, ion and water relations (Naidoo et al. 2011). Forest surveys undertaken in Gazi bay (J. Lang'at et al. unpublished) indicated that Makongeni mangroves were structurally superior to Gazi mangroves (basal area 24.4 m^2 ha^{-1} vs 13.7 m^2 ha^{-1}, respectively).

4.4.2 Belowground Biomass (BGB) Production

Similar to the pattern shown by AGB production, Makongeni mangroves exhibited higher BGB production than those of Gazi. *Avicennia marina* at Makongeni had the highest BGB production (603.2±128.1 g m^{-2} yr^{-1}), followed by *S. alba* (516.0±422.9 g m^{-2} yr^{-1}), Makongeni *R. mucronata* (373.5±119.8 g m^{-2} yr^{-1}), Gazi *R. mucronata* (134.9±48.2 g m^{-2}

yr^{-1}), Gazi *A. marina* (128.2±49.7 g m^{-2} yr^{-1}) and *C. tagal* (64.9±41.0 g m^{-2} yr^{-1}). The BGB production of *S. alba* was highly variable. This was due to a sample which had exceptionally high root mass.

However, these values are within the range reported for a range of mangrove settings (Table 4.7, from riverine to scrub mangroves) (e.g. Sánchez, 2005; McKee *et al.*, 2007a; Castaneda-Moya *et al.*, 2011). However, the root production reported here may be an under-estimate, since root turnover during the in-growth period was not considered and since the limited period of root growth in this study probably precluded the development of very large roots in the in-growth trenches. In terms of the contribution of the root production to the total plant production, *A. marina* at Makongeni had the highest proportion (53.0 %) followed by *S. alba* (44.4 %), *C. tagal* (26.9 %), *A. marina* at Gazi (24.3 %) and *R. mucronata* (16.4 and 19.1 % at Gazi and Makongeni, respectively). These figures are similar to the proportion of belowground biomass reported for mangroves, 30-60 % (e.g. Golley *et al.*, 1962; Komiyama *et al.*, 2008), thereby indicating that plant productivity follow similar patterns to those of plant biomass allocation.

Root production increased significantly with decreasing soil moisture content, increasing redox potential and increasing proportion of coarse soil particles (> 500 μm) (Table 4.3), which was similar to the trend observed for Florida mangroves (Sánchez, 2005). The response of root growth to low soil moisture content could be an adaptive mechanism to increase water and nutrient uptake. Soil moisture influences a number of chemical soil properties such as salinity and the availability of mineral ions (Saenger, 2002). Coarse

textured soils have low nutrients; hence, plants have to increase root density in order to capture more nutrients in such soils. The extensive, albeit shallow, mangrove root system with numerous lenticels and aerenchyma tissue is responsible for oxygen-rich rhizosphere around the roots, which enables aerobic metabolism under generally anaerobic conditions (Tomlinson, 1986; Ball, 1988). The redox status of the sediment influences the form and availability of inorganic nutrients (Ball, 1988); therefore, the modification of soil oxygen status by high root density results in a counter-effect between mangrove productivity and anoxia.

4.4.3   Root:Shoot Production Ratios

Mangrove forests have been shown to have higher RSR than their terrestrial counterparts, ranging from 0.2 to 4.0 (Snedaker, 1995; Saintilan, 1997a; 1997b; Sánchez, 2005; Komiyama *et al.*, 2008; Kauffman *et al.*, 2011) However, the high variability in RSR values between different mangrove forests may indicate that RSR in mangroves and terrestrial forests are similar (Alongi, 2009). *A. marina* (Am-M) had the highest proportion of BGB production of the total production (53 %; range, 44.5-69.2 %).

Table 4.7. Comparison of BGB production of mangrove forests of various places across the world

Forest Type/setting	Dominant species	Latitude	BGB (t ha^{-1} yr^{-1})	Location	Reference
Basin, landward	*Avicennia*	4.65	3.66	Gazi bay, Kenya	This study
Scrub	*Ceriops*	4.65	0.65	Gazi bay, Kenya	"
Basin, interior	*Rhizophora*	4.65	2.54	Gazi bay, Kenya	"
Fringe	*Sonneratia*	4.65	5.16	Gazi bay, Kenya	"
Basin	*Rhizophora and Avicennia*		5.25	Twins Cays, Belize	McKee *et al.* (2007a)
Fringe	*Rhizophora*		3.94	Twins Cays, Belize	"
Transition	*Rhizophora*		0.82	Twins Cays, Belize	"
Fringe	*Rhizophora*		2.65	Rotatan Is., Honduras	Cahoon *et al.*, 2003
Basin	*Avicennia*		3.02	Rotatan Is., Honduras	
Fringe	*Rhizophora*		3.52	US (Florida)	Sanchez, (2005)
Basin	*Rhizophora, Avicennia and Laguncularia*		3.14		"
Basin	*Avicennia*		3.78		"
Scrub	*Rhizophora*		3.07		"
Riverine	*Rhizophora, Laguncaria, Ceriops*	25.82	4.65	Shark River, Florida	Castaneda-Moya et al. (2011)
Riverine	*Rhizophora, Laguncaria, Aegiceras*	25.82	6.43	Shark River, Florida	"
Riverine	*Rhizophora, Laguncaria, Aegiceras*	25.82	4.69	Shark River, Florida	"
Scrub	*Rhizophora*	25.82	5.61	Taylor River, Florida	"
Scrub	*Rhizophora*	25.82	4.07	Taylor River, Florida	"
Fringe	*Rhizophora, Ceriops*	25.82	4.85	Taylor River, Florida	"

Although high biomass does not necessarily equate to high productivity, the below- to aboveground productivity ratios (RSR_p) reported here were similar to the below- to aboveground biomass ratios (RSR) range in mangroves. Therefore, factors influencing RSR may have similar effects in productivity ratios. High RSR in mangroves have been attributed to unstable substratum, and other environmental stressors such as salinity, aridity and nutrient availability (Hutchings and Saenger, 1987; Hutchings and John, 2004; Naidoo, 2009). RSR_p reported here correlated significantly with soil moisture (negative) and redox potential (positive); these two are likely to be significantly correlated themselves, with dryer soils having higher redox potentials (Table 4.3). This was in agreement with the existing evidence that RSR of many trees are sensitive to soil moisture content (Reef *et al.*, 2010), though the degree of sensitivity varies with mangrove species, forest structure and age (Ye *et al.*, 2003; Krauss *et al.*, 2006; Tamooh *et al.*, 2008). Increases in salinity tended to have a positive effect on the RSR_p, although the relationship was weak and only approached significance (R = 0.4, P = 0.075). Soil chemical conditions such as salinity and anoxia influence nutrient availability, with high salinity and low oxygen limiting nutrient acquisition by plants, therefore, plants in highly saline conditions will allocate high investment in belowground roots, resulting in higher RSR (McKee, 1995a; Naidoo, 2009; Reef *et al.*, 2010).

4.5 Conclusions

This study has confirmed that variation exists in productivity between mangrove forest types within a locality. Environmental factors such as salinity influenced aboveground productivity, while soil moisture, texture and anoxia were important factors driving

belowground productivity. Belowground productivity contributed between 20-50 % to the total forest productivity, which was similar to the range of figures reported for mangroves elsewhere. The relationship between the AGB and BGB production was not significant for each forest type. Therefore, further work would be needed to produce a AGB-BGB model that is sufficiently accurate to be use in carbon accounting and forestry management. RSR_P followed similar patterns to above-belowground biomass ratios, implying that factors which influence biomass allocation to belowground plant components also drive the above-belowground productivity ratios.

CHAPTER FIVE: GENERAL CONCLUSIONS

Mangrove forests usually underpin local livelihoods and often have national economic importance in the countries in which they occur. In addition, they offer vital ecological and environmental functions that enhance human wellbeing. Owing to their high productivity (Twilley *et al.*, 1992; Bouillon *et al.*, 2008) and low rates of decomposition in the anoxic sediments (Middleton and McKee, 2001; Huxham *et al.*, 2010b), mangroves are among the most efficient carbon sinks (Donato *et al.*, 2011) and hence offer an opportunity for mitigating climate change (Siikamäki *et al.*, 2012). However, the rapid growth of human populations and the resulting pressure on the coastal environments put mangrove forests at a high risk of disturbance and loss. Over a third of mangroves have been lost in the last 50 years, and much of what remains is in a degraded condition (Valiela *et al.*, 2001; 2009; Spalding *et al.*, 2010; Giri *et al.*, 2011). Despite a recent decrease in the global rate of mangrove loss, mangrove forests are still declining at a higher rate than most other ecosystems (FAO, 2007).

Globally, extraction of wood products accounts for 26 % of mangrove loss, which makes it second to aquaculture (52 %) in importance as a cause of deforestation (Valiela *et al.*, 2001). However, in Kenya and the entire Western Indian Ocean region, over-exploitation for wood products seems to be the leading driver of mangrove loss (Abuodha and Kairo, 2001). Based on a recent analysis, Kenyan mangroves have experienced a loss of 18 % (at 0.7 % yr^{-1}) between 1985 and 2010 (Kirui *et al.*, 2012).

Since mangrove ecosystems are among the most valuable coastal wetland ecosystems (Costanza *et al.*, 1997), their loss has far reaching economic impacts on the coastal populations that depend on them. In addition, other ecological and environmental functions of mangroves will also be substantially impaired by degradation and loss.

5.1   Implications of Unsustainable Harvesting on the Carbon Balance in Mangrove Ecosystems

The effects of large-scale clear-cutting and damage by natural events like hurricanes on the carbon fluxes in mangrove ecosystems have been quantified in some studies (Cahoon *et al.*, 2003; Lovelock *et al.*, 2011; Barr *et al.*, 2012). Clear-cutting or hurricane damage of mangrove forests can also induce subsidence of sediment surface due to enhanced decomposition of organic matter and lack of new growth of roots.

The present study employed small-scale cutting to determine the effects of tree removal on sediment carbon efflux, root decomposition and surface elevation. The results observed indicate that treatment enhanced carbon emissions from mangrove sediments, in excess of 14.2 ± 10.3 tCO_2 ha^{-1} over a period of 530 days (~1.5 yrs) at an average rate of 9.8 ± 7.1 tCO_2 ha^{-1} yr^{-1}. when only heterotrophic respiration (R_H) in control plots was considered, the additional C losses arising from small-scale clear-cutting would be 36.7 ± 10.7 tCO_2 ha^{-1} (mean rate = 25.3 ± 7.4 tCO_2 ha^{-1} yr^{-1}) . Most of the losses were observed within the first year of treatment at the rate of 13.2 ± 9.7 tCO_2 ha^{-1} yr^{-1}, but dropped to 7.9 ± 6.8 tCO_2 ha^{-1} yr^{-1} in the second year after treatment. However, when the heterotrophic respiration in the control plots was considered the treated plots still had higher CO_2 emissions in excess of

28.2 $\pm$5.3 tCO_2 ha^{-1} yr^{-1} and 23.6 $\pm$10.4 tCO_2 ha^{-1} yr^{-1} in the first and second year, respectively. Decomposition of dead roots (induced by treatment) was likely responsible for the increased CO_2 emissions in treated sites. Analysis of stable carbon isotope signatures indicated that the carbon source in the sediment respired CO_2 was from mangrove plant materials (Figure 2.5, Chapter Two) and possibly from oxidation CH_4 produced deeper in the sediment. The fact that sediment surface temperature did not significantly influence CO_2 emissions (Table 2.2, Chapter Two) even though it was significantly high in the treated sites than in the controls throughout the treatment period also supports the possibility of root decomposition enhancing C emissions. The rate of root decomposition in the cut plots showed an increasing trend between 120 and 270 days after burial (0.16 and 0.19 % decay day^{-1}, respectively), while that in the control plots seemed to stabilize at 0.16 % decay day^{-1} between the two retrieval times (Figure 2.6, Chapter Two).

The contribution of root respiration to total sediment respiration was 40.5$\pm$6.4 % (range: 31.2-50.0 %). This was similar to the values reported for temperate vegetated peatlands; 35-57 % (Crow and Wieder, 2005). The contribution of root respiration to total respiration in forest ecosystems averages 48 % (Hanson *et al.*, 2000). However, it should be noted that present study employed an indirect method of estimating the contribution of root respiration, which does not take in to account the CO_2 flux arising from mycorrhizal activities within the rhizosphere, though it is an important component of autotrophic respiration.

Methane emissions were highly variable in both the treated and control plots. However, there was evidence of enhanced emissions in the treated plots, particularly during the girdled period. The high CH_4 emissions in treated plots after girdling was likely due to increased fermentable sugars in the sediment arising from dying labile roots and possibly from falling of leaves induced by girdling. There was also a likelihood that CH_4 was emitted in the deeper profile in the treated plots, but might have been oxidised before reaching the surface. The sediment respired CO_2 was at one point more depleted in ^{13}C (-32‰; Figure 2.3, Chapter Two) than accounted for by C from plant material (-27‰ for mangrove roots), and there are no primary sources of organic material at the field site with stable carbon signatures more depleted than that of mangroves. Methane has been shown to have a light C signature, down to -60‰ (Reeburgh, 2007; Panchuk *et al.*, 2008).

The values of C emissions reported here could be an underestimate of the contribution of autotrophic respiration to total sediment respiration because a) C from root exudates is not included; b) some C released in the rhizosphere is likely to be exported by lateral advection of porewater during ebb tides and c) the possibility of biogenic structures such as aerial roots being conduit within which C may escape in to the atmosphere.

The girdling and cutting treatments also triggered substantial subsidence of up to -51 mm (average rate; 32 mm yr^{-1}); with root decomposition and soil consolidation and/or compaction being the processes likely to have contributed to subsidence. Similarly, the collapse of arenchymatic tissues in the dying plant roots and absence of new root growth might have exacerbated the collapse of the sediment surface. This is also supported by the

slightly higher root decomposition rates in cut plots (~ 0.19 vs 0.16 % loss day^{-1}; Figure 2.6, Chapter Two). Since both the cut and control plots experienced similar rates of accretion (Figure 2.9, Chapter Two) enhanced erosion can be discounted as a possible cause of subsidence. The subsidence of ~ -50 mm in the cut plots led to a loss of ~ 30 tC ha of soil carbon stock within 2 years after treatment, compared to the controls which experienced an elevation of over 10 mm. The subsidence experienced in the cut sites reported here was higher than that found in hurricane impacted mangroves in Honduras (-11 mm yr^{-1}; Cahoon *et al.*, 2003) over a similar period. A simulation of the impacts of hurricanes on mangroves showed that mangrove would experience a subsidence at the rate of -37 mm yr^{-1} 2 years after the impact of storm, which is similar to what is reported here. However the high rates of subsidence recorded in the experimental plots was striking, particularly given their relatively small size. The results of the present experiment suggest managers need to consider carefully the likely impacts of even small scale cutting on surface elevation dynamics and below-ground carbon storage.

5.2   The Implications of Tree Removal on Natural Regeneration and Macrofauna Composition

Natural regeneration is very important in restocking of the mangrove forests and therefore any activity that tampers with this process is bound to compromise the future structural composition of the forest. Selective logging, a system of mangrove pole harvesting employed in eastern Africa, leaves some areas degraded and even denuded if not implemented properly. It is evident that most mangrove forests under concession and/or illegal cutting, particularly in Kenya, have been degraded (Bosire *et al.*, 2003; Dahdouh-

Guebas *et al.*, 2004). This study found that small scale logging, where all the aboveground tree components are removed, would drastically affect the patterns of natural regeneration. However, the presence of seed trees in the logged sites would encourage robust regeneration. This was evident during the girdled period, in which the aboveground tree components were intact, despite the removal of seedlings and saplings. Before dying (~ 4 months after girdling) the girdled trees probably supplied propagules which were responsible for the higher density of juveniles in the treated plots (Table 3.1; Chapter Three). The shedding of leaves induced by girdling opened up the canopy and might have enhanced the robust regeneration observed in the girdled plots. In addition, most of the seedlings which were cut during girdling experienced re-sprouting, which constituted 15 % of the total natural regeneration in the treated plots. However, after cutting, natural regeneration in the treated plots was drastically impaired. Analysis of seedling establishment from the edge of the cut plots indicated that the proximity of seed trees significantly influenced seedling recruitment (Blanchard and Prado, 1995; McKee, 1995b). This would also suggest that propagules of *Rhizophora* display 'self-planting' (Dawes, 1980; Tomlinson, 1986) rather than 'stranding' (e.g. Rabinowitz, 1978), at least at the experimental site. This was contrary to earlier findings for the mangroves of Kenya, which had favoured the 'stranding' theory in over-exploited sites, whilst self-planting was suggested as the preponderant strategy in undisturbed sties (Van Speybroeck, 1992).

Mangrove plants influence species composition and abundance of benthic communities by providing food materials and modifying the microclimate of the mangrove environment. Therefore, removal of tree canopy would drastically affect the distribution and species

composition of these communities. This study found that tree removal enhanced the abundance of gap-dominant species of brachyuran crabs, particularly *U. annulipes* (Figure 3.1, Chapter Three). It is possible that canopy removal might have enhanced microphytobenthic growth, which favour deposit feeders like the majority of *Uca* species. Earlier studies at Gazi bay have shown that a number of *Uca* species prefer open, albeit harsh, areas, particularly in deforested sites (Fondo and Martens, 1998). Similarly, tree canopy removal drastically affected the abundance of gastropods, particularly *C. decollata*. The abundance of this species was significantly reduced in the treated plots. A preference for cool sites provided by canopy cover was the most probable reason why this was the case in the present study.

5.3   Patterns of Mangrove Forest Productivity across Intertidal Gradient

It is now evident that, in addition to being highly productive ecosystems rivalling their terrestrial tropical counterparts, mangrove forests generally allocate a higher proportion of carbon fixed by photosynthesis to belowground root systems (Golley *et al.*, 1962; Twilley *et al.*, 1992; Bouillon *et al.*, 2008; Donato *et al.*, 2011). The partitioning of carbon to various plant components is strongly influenced by environmental factors. Plants growing in nutrient poor soils tend to allocate more carbon to belowground roots to increase the acquisition of the most limiting resources. This is believed to be the case for mangroves since they grow in harsh environments with prevalent stressors such as salinity, hydroperiodism and anoxia.

Globally, mangrove productivity varies latitudinally, with temperature being the main causal agent (Clough, 1992; Saenger and Snedaker, 1993). Within the same climatic zones, the structure and growth of mangroves is controlled by geomorphological characteristics (Thom, 1982). However, soil factors, stand age and site history influence the variations observed in mangrove forest productivity within the same locality (Smith III, 1992; Chen and Twilley, 1999; Sherman *et al.*, 2003). The results from the present study confirmed that there exist variations in mangrove forest productivity within the same locality. There was large variation in both AGB and BGB production between the two sites and between forest types within the Gazi bay mangrove ecosystem. The mangroves of Makongeni, bounded by two creeks and a wider intertidal area, had higher biomass production than those of Gazi, which has a narrow intertidal area. The geomorphological configurations of the bay might have partially contributed to the variation in biomass between the two sites. *Rhizophora mucronata* forest had the highest AGB production; whilst *A. marina* had the highest BGB production. The productivity of these mangrove species were similar to those reported elsewhere for mangroves. Salinity, redox potential and soil moisture appeared to be the most important soil factors influencing productivity. Aboveground biomass production appeared to decrease with increasing salinity, which was similar to findings from studies elsewhere and at Gazi, where soil salinity has been shown as the key factor regulating early survival and growth of high shore trees (Kirui *et al.*, 2008). On the other hand, BGB production increased with decreasing soil moisture content, increasing redox potential and proportion of large soil particles. This study also found that the BGB production of the four mangrove forest types contributed to between 16 to 53 % to the total plant production, which appeared to follow similar patterns to those of plant biomass allocation. The RSRp,

which ranged from 0.20 (*R. mucronata*) to 1.35 (*S. alba*), was influenced by soil moisture content (negative) and redox potential (positive).

The relationship between AGB and BGB production for each mangrove forest types assessed was not significant. Hence, further work need to be conducted to come up with reliable proxies for estimating belowground production. Developing proxies for estimating the belowground productivity of mangroves is very important because of the methodological difficulties involved in using direct methods. Therefore, results from this study form a useful baseline for future research on refining belowground productivity estimation techniques, especially for carbon accounting and climate change mitigation initiatives.

5.4   Mangrove Forest Management Options

The importance of mangrove resources to the local people is well documented (e.g. Wass, 1995; Dahdouh-Guebas *et al.*, 2000; Walters, 2005; 2008). Because of their high productivity and hence efficiency in carbon storage (e.g. Twilley *et al.*, 1992; Bouillon *et al.*, 2008; Donato *et al.*, 2011), mangroves offer potential candidates for carbon offset initiatives that are geared towards climate change mitigation. However, due to the increase in population and associated pressures on coastal resources, carbon stored in mangroves and other blue carbon ecosystems (i.e. vegetated ecosystems in the oceans) are at a high risk. This study has shown that un-controlled logging in mangrove forests might not only result in reduced wood quality, but may also drastically impair the environmental and ecological functioning of mangroves. The release of additional of ~ 14.2 tCO_2 ha^{-1} and

subsidence of down to -51 mm in ~ 2 years in response to this small scale experimental cutting does not augur well for the functionality of mangroves suffering larger scale disturbances. However, this study has also confirmed the notion that mangrove forests are very productive ecosystems, rivalling their terrestrial counterparts. It has been shown that preventing further loss and degradation of vegetated intertidal ecosystems such as mangroves, seagrass beds and saltmarshes could contribute to offsetting between 3-7 % of carbon emissions due to fossil fuel burning (Donato *et al.*, 2011; McLeod *et al.*, 2011). Therefore, mangrove managers, including in Kenya and the Western Indian Ocean, ought to put in place management options that would ensure sustainability of mangrove resources as well as other benefits such as biodiversity conservation and carbon sequestration. This would include developing management plans that would assist local populations in the sustainable utilization of mangrove products, with concerted efforts towards rehabilitating degraded sites and enhancing regeneration in utilization zones.

Similarly, financial initiatives such as Reducing Emissions from Deforestation and Degradation and conservation of forest ecosystems (REDD+) are postulated as new ways to achieve additional income from forest conservation. Accounting for carbon storage in and efflux from forest ecosystems is crucial to the implementation of climate change mitigation programmes such as REDD+ (Keith *et al.*, 2009; Donato *et al.*, 2011). In addition to this, managers and other stakeholders could engage in exploring the opportunities of establishing payment for ecosystem services (PES) schemes in mangrove ecosystems. Despite the documented importance of mangrove ecosystems, particularly in terms of carbon storage, very little effort has been made in incorporating them in financial initiatives

such as REDD+ and PES (Kairo, 2008). PES schemes such as selling carbon credits through the voluntary carbon markets offer the local communities living in the vicinity of mangrove forests the opportunity to improve their livelihoods by engaging in conservation activities. The 2005 Forest Act of Kenya promotes the participation of local population in the management of forest ecosystems in their immediate surroundings (MENR, 2007). The participation of local communities in natural resources management coupled with benefits sharing would ensure the achievements of the goals envisioned by the Kenya Vision 2030 strategic plans (GOK, 2007).

For such participatory forest management schemes to be effective, the establishment of a sound scientific basis is crucial. Therefore, this study concludes with the following recommendations as key objectives for future work:

a) Determination of total C losses including dissolved inorganic carbon (DIC) in mangrove ecosystems in order to accurately determine their carbon budgets.

b) Developing and refining methodologies for estimating mangrove forest productivity, particularly belowground productivity, in the Western Indian Oceans.

c) Developing mangrove management plans that factor in integrated management to cater for human wellbeing and ecosystem health of the coastal habitats.

d) Promoting and encouraging community-based mangrove forest conservation and management.

REFERENCES

Abuodha, P. and Kairo, J. G. (2001). Human-induced stresses on mangrove swamps along Kenya coast. *Hydrobiologia*, **458:** 255-265.

Alfaro, A. C., Thomas, F., Sergent, L. and Duxbury, M. (2006). Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. *Estuarine, Coastal and Shelf Science*, **70:** 271-286.

Alongi, D., de Carvalho, N., Amaral, A., Costa, A., Trott, L. and Tirendi, F. (2012). Uncoupled surface and below-ground soil respiration in mangroves: implications for estimates of dissolved inorganic carbon export. *Biogeochemistry*, **109:** 151-162.

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, Netherlands. 216 p.

Alongi, D. M. (2012). Carbon sequestration in mangrove forests. *Carbon Management*, **3:** 313-322.

Alongi, D. M. and Brinkman, R. (2011). Hydrology and Biogeochemistry of Mangrove Forests, *In* Levia, D. F., Carlyle-Moses, D. and Tanaka, T. [eds.], *Forest Hydrology and Biogeochemistry*. Ecological Studies. Springer Netherlands. pp. pp. 203-219.

Alongi, D. M., Clough, B. F. and Robertson, A. I. (2005). Nutrient-use efficiency in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Aquatic Botany*, **82:** 121-131.

Alongi, D. M. and de Carvalho, N. A. (2008). The effect of small-scale logging on stand characteristics and soil biogeochemistry in mangrove forests of Timor Leste. *Forest Ecology and Management*, **255:** 1359-1366.

Alongi, D. M. and Dixon, P. (2000). Mangrove primary production and below-ground biomass in Sawi Bay, Southern Thailand. *Phuket Marine Biological Center Special Publication*, **22:** 31-38.

Alongi, D. M., Sasekumar, A., Chong, V. C., Pfitzner, J., Trott, L. A., Tirendi, F., Dixon, P. and 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.

Alongi, D. M., Tirendi, F. and Clough, B. F. (2000). Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and Avicennia marina along the arid coast of Western Australia. *Aquatic Botany*, **68:** 97-122.

Amarasinghe, M. D. and Balasubramaniam, S. (1992). Net primary productivity of two mangrove forest stands on the northwestern coast of Sri Lanka. *Hydrobiologia*, **247:** 37-47.

Andersen, C., Nikolov, I., Nikolova, P., Matyssek, R. and Häberle, K.-H. (2005). Estimating "autotrophic" belowground respiration in spruce and beech forests: decreases following girdling. *European Journal of Forest Research*, **124:** 155-163.

Andersen, F. Ø. and Kristensen, E. (1988). Oxygen microgradients in the rhizosphere of the mangrove *Avicennia marina* (Forsk.) Vierh. *Marine Ecology Progress Series*, **44:** 201-204.

Andrews, J. A., Harrison, K. G., Matamala, R. and Schlesinger, W. H. (1999). Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). *Soil Sci Soc Am J*, **63:** 1429-1435.

Andriesse, J. P. (1988). *Nature and Management of Tropical Peat Soils*. FAO Soils Bulletin 59, Food and Agriculture Organisation of the United Nations, Rome, Italy. 165 p.

Baggs, E. (2006). Partitioning the components of soil respiration: a research challenge. *Plant and Soil*, **284:** 1-5.

Baldwin, A., Egnotovich, M., Ford, M. and Platt, W. (2001). Regeneration in fringe mangrove forests damaged by Hurricane Andrew. *Plant Ecology*, **157:** 151-164.

Barr, J. G., Engel, V., Smith, T. J. and Fuentes, J. D. (2012). Hurricane disturbance and recovery of energy balance, CO_2 fluxes and canopy structure in a mangrove forest of the Florida Everglades. *Agricultural and Forest Meteorology*, **153:** 54-66.

Bhupinderpal-Singh, Nordgren, A., Lofvenius, M. O., Hogberg, M. N., Mellander, P.-E. and Hogberg, P. (2003). Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant, Cell & Environment*, **26:** 1287-1296.

Binkley, D., Stape, J., Takahashi, E. and Ryan, M. (2006). Tree-girdling to separate root and heterotrophic respiration in two *Eucalyptus* stands in Brazil. *Oecologia*, **148:** 447-454.

Blanchard, J. and Prado, G. (1995). Natural regeneration of *Rhizophora mangle* in strip clearcuts in northwest Ecuador. *Biotropica*, **27:** 160-167.

Blanco, J. F., Estrada, E. A., Ortiz, L. F. and Urrego, L. E. (2012). Ecosystem-wide impacts of deforestation in mangroves: The Urabá Gulf (Colombian Caribbean) case study. *ISRN Ecology*, **2012:** 14 pages.

Blodau, C. (2002). Carbon cycling in peatlands - A review of processes and controls. *Environmental Reviews*, **10:** 111-134.

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

Bosire, J. O., Kairo, J. G., Kazungu, J., Koedam, N. and Dahdouh-Guebas, F. (2008). Spatial and temporal regeneration dynamics in *Ceriops tagal* (Perr.) C.B. Rob. (Rhizophoraceae) mangrove forests in Kenya. *Western Indian Ocean Journal of Marine Science*, **7:** 69-80.

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. and Twilley, R. R. (2008). Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles*, **22:** GB2013, doi:2010.1029/2007GB003052.

Breithaupt, J. L., Smoak, J. M., Smith III, T. J., Sanders, C. J. and Hoare, A. (2012). Organic carbon burial rates in mangrove sediments: Strengthening the global budget. *Global Biogeochemical Cycles***:** doi:10.1029/2012GB004375, in press.

Briggs, S. V. (1977). Estimates of biomass in a temperate mangrove community. *Austral Ecology*, **2:** 369-373.

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

Burford, M. A. and Longmore, A. R. (2001). High ammonium production from sediments in hypereutrophic shrimp ponds. *Marine Ecology Progress Series*, **224:** 187-195.

Cahoon, D. R., Hensel, P., Rybczyk, J., McKee, K. L., Proffitt, C. E. and Perez, B. C. (2003). Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology*, **91:** 1093-1105.

Cahoon, D. R. and Lynch, J. C. (1997). Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, U.S.A. *Mangroves and Salt Marshes*, **1:** 173-186.

Cairns, M. A., Brown, S., Helmer, E. H. and Baumgardner, G. A. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, **111:** 1-11.

Castaneda-Moya, E., Twilley, R., Rivera-Monroy, V., Marx, B., Coronado-Molina, C. and Ewe, S. (2011). Patterns of root dynamics in mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. *Ecosystems*, **14:** 1178-1195.

Cerone, P. and Dragomir, S. S. (2000). Trapezoidal-type rules from an inequalities point of view, *In* Anastassiou, G. [ed.], *Handbook of Analytic-Computational Methods in Applied Mathematics*. CRC Press. pp. 65-134.

Chapin III, F. S., Bloom, A. J., Field, C. B. and Waring, R. H. (1987). Plant responses to multiple environmental factors. *BioScience*, **37:** 49-57.

Chen, G. C., Tam, N. F. Y. and Ye, Y. (2010). Summer fluxes of atmospheric greenhouse gases N_2O, CH_4 and CO_2 from mangrove soil in South China. *Science of The Total Environment*, **408:** 2761-2767.

Chen, R. and Twilley, R. R. (1999). A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry*, **44:** 93-118.

Chmura, G. L., Anisfeld, S. C., Cahoon, D. R. and Lynch, J. C. (2003). Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, **11:** 1111-11120.

Christensen, B. (1978). Biomass and primary production of Rhizophora apiculata Bl. in a mangrove in southern Thailand. *Aquatic Botany*, **4:** 43-52.

Cintron, G. and Schaeffer-Novelli, Y. (1984). Methods for studying mangrove structure, *In* Snedaker, S. C. and Snedaker, J. G. [eds.], *The Mangrove Ecosystem: Research Methods*. pp. 91 -113.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18:** 117-143.

Clarke, K. R. and Green, R. H. (1988). Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series***:** 213-226.

Clarke, K. R. and Warwick, R. M. (1994). *Changes in Marine Communities:an Approach to Statistical Analysis and Interpretation.* Plymouth Marine Laboratory, UK. 144 p.

Clough, B. F. (1992). Primary productivity and growth of mangrove forests, *In* Robertson, A. I. and Alongi, D. M. [eds.], *Tropical mangrove Ecosystems*. America Geophysical Union. pp. 225-249.

Clough, B. F., Ong, J. E. and Gong, W. K. (1997). Estimating leaf area index and photosynthetic production in canopies of the mangrove *Rhizophora apiculata*. *Marine Ecology Progress Series*, **159:** 285-292.

Clough, B. F. and Sim, R. G. (1989). Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. *Oecologia*, **79:** 38-44.

Comley, B. W. T. and McGuiness, K. A. (2005). Above- and below-ground biomass, and allometry, of four common northern Australian mangroves. *Australian Journal of Botany*, **53:** 431-436.

Comstedt, D., Boström, B. and Ekblad, A. (2010). Autotrophic and heterotrophic soil respiration in a Norway spruce forest: estimating the root decomposition and soil moisture effects in a trenching experiment. *Biogeochemistry***:** 1-12.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. and van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, **387:** 253-260.

Couwenberg, J., Dommain, R. and Joosten, H. (2010). Greenhouse gas fluxes from tropical peatlands in south-east Asia. *Global Change Biology*, **16:** 1715-1732.

Crow, S. E. and Wieder, R. K. (2005). Sources of CO_2 emission from a northern peatland: Root respiration, exudation and decomposition. *Ecology*, **86:** 1825-1834.

Dahdouh-Guebas, F., Mathenge, C., Kairo, J. G. and 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., Van Pottelbergh, I., Kairo, J. G., Cannicci, S. and Koedam, N. (2004). 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.

Dawes, C. J. (1980). *Marine Botany*. John Wiley and Sons, New York. 628 p.

Day, J. W., Conner, W. H., Ley-Lou, F., Day, R. H. and Navarro, A. M. (1987). The productivity and composition of mangrove forests, Laguna de Términos, Mexico. *Aquatic Botany*, **27:** 267-284.

Day, J. W., Coronado-molina, C., Vera-Herrera, F. R., Twilley, R., Rivera-Monroy, V. H., Alvarez-Guillen, H., Day, R. and Conner, W. (1996). A 7-year record of above-ground net primary production in a southeastern Mexican mangrove forest. *Aquatic Botany*, **55:** 39-60.

Dittmar, T., Hertkorn, N., Kattner, G. and Lara, R. J. (2006). Mangroves, a major source of dissolved organic carbon to the oceans. *Global Biogeochemical Cycles*, **20:** GB1012, doi:1010.1029/2005GB002570.

Dixon, R. K., Solomon, A. M., Brown, S., Houghton, R. A., Trexier, M. C. and Wisniewski, J. (1994). Carbon pools and flux of global forest ecosystems. *Science*, **263:** 185-190.

Donato, D. C., Kauffman, J. B., Mackenzie, R. A., Ainsworth, A. and Pfleeger, A. Z. (2012). Whole-island carbon stocks in the tropical Pacific: Implications for mangrove conservation and upland restoration. *Journal of Environmental Management*, **97:** 89-96.

Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., Stidham, M. and Kanninen, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, **4:** 293-297.

Doute, R. N., Ochanda, N. and Epp, H. (1981). A forest inventory using remote sensing technique. Technical Report, Series No. 30. Kenya Rangelands Ecological Monitoring Unit, Department of Remote Sensing, Nairobi.

Duke, N. C. (1992). Mangrove floristics and biogeography, *In* Robertson, A. I. and Alongi, D. M. [eds.], *Tropical Mangrove Ecosystems*. Coastal Estuarine Studies. AGU. pp. 63-100.

Edwards, N. T. and Harris, W. F. (1977). Carbon cycling in a mixed deciduous forest floor. *Ecology*, **58:** 431-437.

Edwards, N. T. and Ross-Todd, B. M. (1979). The effects of stem girdling on biogeochemical cycles within a mixed deciduous forest in eastern Tennessee. I. Soil solution chemistry, soil respiration, litterfall and root biomass studies. *Oecologia*, **40:** 247-257.

Ekblad, A., Nyberg, G. and Högberg, P. (2002). ^{13}C-discrimination during microbial respiration of added C_3-, C_4- and ^{13}C-labelled sugars to a C_3-forest soil. *Oecologia*, **131:** 245-249.

Epron, D., Le Dantec, V., Dufrene, E. and Granier, A. (2001). Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. *Tree Physiol*, **21:** 145-152.

Ewel, K. C., Twilley, R. and Ong, J. E. (1998a). Different kinds mangrove forest provides different goods and services. *Global Ecology and Biogeography Letters*, **7:** 83-94.

Ewel, K. C., Zheng, S., Pinzon, Z. S. and Bourgeois, J. A. (1998b). Environmental effects of canopy gap formation in high-rainfall mangrove forests. *Biotropica*, **30:** 510-518.

FAO (Food and Agriculture Organization). (1994). Mangrove Forest Management Guidelines. FAO Forestry Paper 117. FAO, Rome. 350 p.

FAO (Food and Agriculture Organization). (2007). The World's Mangroves, 1980-2005: A Thematic Study in the Framework of the Global Forest Resources Assessment 2005. Forestry Paper 153. FAO, Rome. ix + 77 p.

Farnsworth, E. J. and Ellison, A. M. (1997). The global conservation status of mangroves. *Ambio* **26:** 328-334.

Feller, I. C., McKee, K. L., Whigham, D. F. and O'Neill, J. P. (2003a). Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry*, **62:** 145-175.

Feller, I. C., Whigham, D. F., McKee, K. L. and Lovelock, C. E. (2003b). Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia*, **134:** 405-414.

Ferwerda, J., Ketner, P. and McGuinness, K. (2007). Differences in regeneration between hurricane damaged and clear-cut mangrove stands 25 years after clearing. *Hydrobiologia*, **591:** 35-45.

Fondo, E. N. and Martens, E. E. (1998). Effects of mangrove deforestation on macrofaunal densities, Gazi Bay, Kenya. *Mangroves and Salt Marshes*, **2:** 75-83.

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

Fujimoto, K., Imaya, A., Tabuchi, R., Kuramoto, S., Utsugi, H. and Murofushi, T. (1999). Belowground carbon storage of Micronesian mangrove forests. *Ecological Research*, **14:** 409-413.

Gallin, E., Coppejans, E. and Beeckman, H. (1989). The mangrove vegetation of Gazi bay (Kenya). *Bulletin de la Société Royale de Botanique de Belgique*, **122:** 197-207.

Gelman, A. and Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, USA. 648 p.

Gibbs, H. K., Brown, S., Niles, J. O. and Foley, J. A. (2007). Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Journal of Environmental Research Letters*, **2**.

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

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

Gleason, S. M. and Ewel, K. C. (2002). Organic matter dynamics on the forest floor of a Micronesian mangrove forest: An investigation of species composition shifts. *Biotropica*, **34:** 190-198.

Gleeson, S. K. and Tilman, D. (1992). Plant allocation and the multiple limitation hypothesis. *The American Naturalist*, **139:** 1322-1343.

GOK (2007). Kenya Vision 2030. Government of the Republic of Kenya. 32.

Golley, F., Odum, H. T. and Wilson, R. F. (1962). The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology*, **43:** 9-19.

Goreau, T. J. and de Mello, W. Z. (2007). Mininmizing net greenhouse gas sources from mangrove and wetland soils, *In* Tateda, Y. [ed.], *Greenhouse Gas and Carbon Balances in Mangrove Coastal Ecosystems*. pp. pp. 239-248.

Granek, E. and Ruttenberg, B. I. (2008). Changes in biotic and abiotic processes following mangrove clearing. *Estuarine, Coastal and Shelf Science*, **80:** 555-562.

Gullison, R. E., Frumhoff, P. C., Canadell, J. G., Field, C. B., Nepstad, D. C., Hayhoe, K., Avissar, R., Curran, L. M., Friedlingstein, P., Jones, C. D. and Nobre, C. (2007). Environment: Tropical Forests and Climate Policy. *Science*, **316:** 985-986.

Hamilton, J., DeLucia, E., George, K., Naidu, S., Finzi, A. and Schlesinger, W. (2002). Forest carbon balance under elevated CO_2. *Oecologia*, **131:** 250-260.

Hanson, P. J., Edwards, N. T., Garten, C. T. and Andrews, J. A. (2000). Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry*, **48:** 115-146.

Hemminga, M. A., Slim, F. J., Kazungu, J., Ganssen, G. M., Nieuwenhuize, J. and Kruyt, N. M. (1994). Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs at Gazi bay, Kenya. *Marine Ecology Progress Series*, **106:** 291-301.

Hockett, J. C. and Kritzler, H. (1972). Capture-recapture methods with *Uca*. *Biological Bulletin*, **142:** 49-56.

Högberg, P., Bhupinderpal, S., Löfvenius, M. O. and Nordgren, A. (2009). Partitioning of soil respiration into its autotrophic and heterotrophic components by means of tree-

girdling in old boreal spruce forest. *Forest Ecology and Management*, **257:** 1764-1767.

Hogberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Hogberg, M. N., Nyberg, G., Ottosson-Lofvenius, M. and Read, D. J. (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411:** 789-792.

Houghton, R. A. (2005). Tropical deforestation as a source of greenhouse gas emissions, *In* Moutinho, P. and Schwartzman, S. [eds.], *Tropical Deforestation and Climate Change*. Amazon Institute of Environmental Research (IPAM). pp. pp. 13-21.

Houghton, R. A. (2007). Balancing the global carbon budget. *Annual Review of Earth and Planetary Sciences*, **35:** 313-347.

Houghton, R. J. A., Skole, D. L., Nobre, C. A., Hackler, J. L., Lawrence, K. T. and Chomentowski, W. H. (2000). Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature*, **403:** 301-304.

Hutchings, M. J. and John, E. A. (2004). The effects of environmental heterogeneity on root growth and root/shoot partitioning. *Annals of Botany*, **94:** 1-8.

Hutchings, P. and Saenger, P. (1987). *Ecology of Mangroves*. University of Queensland Press, Brisbane. 388 p.

Huxham, M., Kumara, M. P., Jayatissa, L. P., Krauss, K. W., Kairo, J., Langat, J., Mencuccini, M., Skov, M. W. and Kirui, B. (2010a). Intra- and interspecific facilitation in mangroves may increase resilience to climate change threats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365:** 2127-2135.

Huxham, M., Langat, J., Tamooh, F., Kennedy, H., Mencuccini, M., Skov, M. W. and Kairo, J. (2010b). Decomposition of mangrove roots: Effects of location, nutrients, species identity and mix in a Kenyan forest. *Estuarine, Coastal and Shelf Science*, **88:** 135-142.

Jennerjahn, T. C. and Ittekkot, V. (2002). Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften*, **89:** 23-30.

Kairo, J. G. (2008). Experiences with PES in Kenya, *In* Holopainen, J. and Wit, M. [eds.], *Financing Sustainable Forest Management*. Tropenbos International. pp. pp. 107-111.

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

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

Kauffman, J., Heider, C., Cole, T., Dwire, K. and Donato, D. (2011). Ecosystem carbon stocks of Micronesian mangrove forests. *Wetlands*, **31:** 343-352.

Kayler, Z., Ganio, L., Hauck, M., Pypker, T., Sulzman, E., Mix, A. and Bond, B. (2010). Bias and uncertainty of $\delta^{13}CO_2$ isotopic mixing models. *Oecologia*, **163:** 227-234.

Keith, H., Mackey, B. G. and Lindenmayer, D. B. (2009). Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, **106:** 11635-11640.

Kirui, B., Kairo, J. G. and Karachi, M. (2006). Allometric equations for estimating above ground biomass of *Rhizophora mucronata* **Lamk**. (Rhizophoraceae) mangroves at Gazi Bay, Kenya. *Western Indian Ocean Journal of Marine Science*, **5:** 27-34.

Kirui, B. Y. K., Huxham, M., Kairo, J. and Skov, M. (2008). Influence of species richness and environmental context on early survival of replanted mangroves at Gazi bay, Kenya. *Hydrobiologia*, **603:** 171-181.

Kirui, K. B., Kairo, J. G., Bosire, J., Viergever, K. M., Rudra, S., Huxham, M. and Briers, R. A. (2012). Mapping of mangrove forest land cover change along the Kenya coastline using Landsat imagery. *Ocean and Coastal Management***:** doi:10.1016/j.ocecoaman.2011.1012.1004.

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.

Komiyama, A., Havanond, S., Srisawatt, W., Mochida, Y., Fujimoto, K., Ohnishi, T., Ishihara, S. and Miyagi, T. (2000). Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) C. B. Rob.) forest. *Forest Ecology and Management*, **139:** 127-134.

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

Komiyama, A., Ongino, K., Aksornkoae, S. and Sabhasri, S. (1987). Root biomass of a forest in Southern Thailand. 1. Estimation by trench method and zonal structure of root biomass. *Journal of Tropical Ecology*, **3:** 97-108.

Kon, K., Kurokura, H. and Tongnunui, P. (2010). Effects of the physical structure of mangrove vegetation on a benthic faunal community. *Journal of Experimental Marine Biology and Ecology*, **383:** 171-180.

Krauss, K., Doyle, T., Twilley, R., Rivera-Monroy, V. and Sullivan, J. (2006). Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia*, **569:** 311-324.

Kristensen, E. (2007). Carbon balance in mangrove sediments: The driving processes and their controls, *In* Tateda, Y. [ed.], *Greenhouse gas and carbon balances in mangrove coastal ecosystems,*. Gendai Tosho. pp. pp 61-78.

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

Kristensen, E., Flindt, M. R., Ulomi, S., Borges, A. V., Abril, G. and Bouillon, S. (2008b). Emission of CO_2 and CH_4 to the atmosphere by sediments and open waters in two Tanzanian mangrove forests. *Marine Ecology Progress Series*, **370:** 53-67.

Kruskal, J. and Wish, M. (1978). *Multidimensional Scaling*. Sage Publications, Beverly Hills, London. 93 p.

Kucera, C. L. and Kirkham, D. R. (1971). Soil respiration studies in tallgrass prairie in Missouri. *Ecology*, **52:** 912-915.

Laffoley, D. d. A. and Grimsditch, G. [eds.]. (2009). *The management of natural coastal carbon sinks*. IUCN. 53 pp.

Lin, G. and Ehleringer, J. R. (1997). Carbon isotopic fractionation does not occur during dark respiration in C_3 and C_4 plants. *Plant Physiology*, **114:** 391-394.

Lin, G., Ehleringer, J. R., Rygiewicz, P. T., Johnson, Mark G. and Tingey, David T. (1999). Elevated CO_2 and temperature impacts on different components of soil CO_2 efflux in Douglas-fir terracosms. *Global Change Biology*, **5:** 157-168.

Lin, Y.-M., Liu, X.-W., Zhang, H., Fan, H.-Q. and Lin, G.-H. (2010). Nutrient conservation strategies of a mangrove species *Rhizophora stylosa* under nutrient limitation. *Plant and Soil*, **326:** 469-479.

Lovelock, C. (2008). Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems*, **11:** 342-354.

Lovelock, C. E., Ruess, R. W. and Feller, I. C. (2011). CO_2 efflux from cleared mangrove peat. *PLoS ONE*, **6:** e21279.

Lugo, A. E. (1990). Fringe wetlands, *In* Lugo, A. E., Brinson, M. M. and Brown, S. [eds.], *Ecosystems of the World*. Forested Wetlands. Elsevier. pp. 143-169.

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

Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E.-D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J.-M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., GrÜNwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyra, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O., Saigusa,

N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M.-L., Tang, J., Valentini, R., Vesala, T. and Janssens, I. A. (2007). CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13:** 2509-2537.

Machiwa, J. F. and Hallberg, R. O. (1995). Flora and crabs in a mangrove forest partly distorted by human activities, Zanzibar. *Ambio*, **24:** 492-496.

Macintosh, D. J., Ashton, E. C. and Havanon, S. (2002). Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong Mangrove Ecosystem, Thailand. *Estuarine, Coastal and Shelf Science*, **55:** 331-345.

Malhi, Y., Baldocchi, D. D. and Jarvis, P. G. (1999). The carbon balance of tropical, temperate and boreal forests. *Plant, Cell & Environment*, **22:** 715-740.

Matsui, N. (1998). Estimated stocks of organic carbon in mangrove roots and sediments in Hinchinbrook Channel, Australia. *Mangrove and Salt Marshes*, **2:** 199-204.

McKee, K. L. (1995a). Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: Response to light and nutrient availability. *American Journal of Botany*, **82:** 299-307.

McKee, K. L. (1995b). Seedling recruitment patterns in a Belizean mangrove forest: Effects of establishment ability and physico-chemical factors. *Oecologia*, **101:** 448-460.

McKee, K. L. (2001). Root proliferation in decaying roots and old root channels: A nutrient conservation mechanism in oligotrophic mangrove forests? *The Journal of Ecology*, **89:** 876-887.

McKee, K. L. (2011). Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science*, **91:** 475-483.

McKee, K. L., Cahoon, D. R. and Feller, I. (2007a). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, **16:** 545-556.

McKee, K. L., Cahoon, D. R. and Feller, I. (2007b). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, **16:** 545-556.

McKee, K. L. and Faulkner, P. L. (2000). Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. *Atoll Research Bulletin*, **468:** 46-58.

McKee, K. L., Rooth, J. E. and Feller, I. C. (2007c). Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. *Ecological Applications*, **17:** 1678-1693.

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H. and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment*, **9:** 552-560.

MEA (Millennium Ecosystem Assessment). (2005). *Ecosystems and Human Well-being: Biodiversity Synthesis* World Resources Institute, Washington, DC.

MENR (Ministry of Environment and Natural Resources). (1994). Kenya Forest Master Plan; Development Programmes. Department, F., Ministry of Environment and Natural Resources, Government of Kenya, Nairobi, Kenya. 422 p.

MENR (Ministry of Environment and Natural Resources). (2007). Participatory Forest Management Guidelines. Government of the Republic of Kenya, Nairobi, Kenya. 48.

Middleton, B. A. and McKee, K. L. (2001). Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *Journal of Ecology*, **89:** 818-828.

Miller, J. B. and Tans, P. P. (2003). Calculating isotopic fractionation from atmospheric measurements at various scales. *Tellus B*, **55:** 207-214.

Miyajima, T., Y. Tsuboi, Tanaka, Y. and Koike., I. (2009). Export of inorganic carbon from two Southeast Asian mangrove forests to adjacent estuaries as estimated by the stable isotope composition of dissolved inorganic carbon. *Journal of Geophysical Research*, **114:** G01024, doi:01010.01029/02008JG000861.

Mouton, E. C. and Felder, D. L. (1996). Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. *Estuaries*, **19:** 51-61.

Mukhopadhyay, S. K., Biswas, H., De, T. K., Sen, B. K., Sen, S. and Jana, T. K. (2002). Impact of Sundarban mangrove biosphere on the carbon dioxide and methane mixing ratios at the NE Coast of Bay of Bengal, India. *Atmospheric Environment*, **36:** 629-638.

Naidoo, G. (2009). Differential effects of nitrogen and phosphorus enrichment on growth of dwarf Avicennia marina mangroves. *Aquatic Botany*, **90:** 184-190.

Nellemann, C., Corcoran, E., Duarte, C. M., Valdés, L., De Young, C., Fonseca, L. and Grimsditch, G. [eds.]. (2009). *Blue Carbon*. United Nations Environment Programme. 80 p.

Nobbs, M. (2003). Effects of vegetation differ among three species of fiddler crabs (Uca spp.). *Journal of Experimental Marine Biology and Ecology*, **284:** 41-50.

Ong, J.-E., Gong, W. K. and Clough, B. F. (1995). Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* Bl. mangrove forest. *Journal of Biogeography*, **22:** 417-424.

Ong, J. (1993). Mangroves - A carbon source and sink. *Chemosphere*, **27:** 1097-1107.

Panchuk, K., Ridgwell, A. and Kump, L. R. (2008). Sedimentary response to Paleocene-Eocene Thermal Maximum carbon release: A model-data comparison. *Geology*, **36:** 315-318.

Poungparn, S., Komiyama, A., Tanaka, A., Sangtiean, T., Maknual, C., Kato, S., Tanapermpool, P. and Patanaponpaiboon, P. (2009). Carbon dioxide emission through soil respiration in a secondary mangrove forest of eastern Thailand. *Journal of Tropical Ecology*, **25:** 393-400.

Purvaja, R. and Ramesh, R. (2000). Human impacts on methane emission from mangrove ecosystems in India. *Regional Environmental Change*, **1:** 86-97.

Purvaja, R. and Ramesh, R. (2001). Natural and anthropogenic methane emission from coastal wetlands of South India. *Environmental Management*, **27:** 547-557.

Rabinowitz, D. (1978). Dispersal properties of mangrove propagules. *Biotropica*, **10:** 47-57.

Raich, J. W. and Schlesinger, W. H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B*, **44:** 81-99.

Reeburgh, W. S. (2007). Oceanic methane biogeochemistry. *Chemical Reviews*, **107:** 486-513.

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

Richmond, M. D. [ed.]. (2011). *A Field Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands*, Third Edition ed. Sida/WIOMSA. 464 p.

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

Robinson, D. and Scrimgeour, C. M. (1995). The contribution of plant C to soil CO_2 measured using ^{13}C. *Soil Biology and Biochemistry*, **27:** 1653-1656.

Rodeghiero, M. and Cescatti, A. (2006). Indirect partitioning of soil respiration in a series of evergreen forest ecosystems. *Plant and Soil*, **284:** 7-22.

Ross, M. S., Ruiz, P. L., Telesnicki, G. J. and Meeder, J. F. (2001). Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (U.S.A.). *Wetlands Ecology and Management*, **9:** 27-37.

Roth, L. C. (1992). Hurricanes and mangrove regeneration: Effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. *Biotropica*, **24:** 375-384.

Saenger, P. (1982). Morphological, anatomical and reproductive adaptations of Australian mangroves, *In* Clough, B. F. [ed.], *Mangrove Ecosystems in Australia*. Australian National University Press. pp. 153-191.

Saenger, P. and Snedaker, S. C. (1993). Pantropical trends in mangrove above-ground biomass and annual litter fall. *Oecologia*, **96:** 293-299.

Saintilan, N. (1997a). Above- and below-ground biomass of mangroves in a sub-tropical estuary. *Marine and Freshwater Research*, **48:** 601-604.

Saintilan, N. (1997b). Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine Freshwater Research*, **48:** 147-152.

Sánchez, B. G. (2005). *Belowground productivity of mangrove forests in Southwest Florida*. Ph.D. Dissertation. Department of Oceanography and Coastal Sciences, Louisiana State University and Agricultural and Mechanical College. 189 p.

Sapronov, D. and Kuzyakov, Y. (2007). Separation of root and microbial respiration: Comparison of three methods. *Eurasian Soil Science*, **40:** 775-784.

Sasekumar, A. (1974). Distribution of macrofauna on a Malayan mangrove shore. *Journal of Animal Ecology*, **43:** 51-69.

Schlesinger, W. H. (1997). *Biogeochemistry: an analysis of global change*, 2nd ed. Academic, New York.

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

Sherman, R. E., Fahey, T. J. and Battles, J. J. (2000). Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Journal of Ecology*, **88:** 165-178.

Sherman, R. E., Fahey, T. J. and Martinez, P. (2001). Hurricane impacts on a mangrove forest in the Dominican Republic: damage patterns and early recovery. *Biotropica*, **33:** 393-408.

Sherman, R. E., Fahey, T. J. and Martinez, P. (2003). Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems*, **6:** 384-398.

Siikamäki, J., Sanchirico, J. N. and Jardine, S. L. (2012). Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences*.

Skilleter, G. A. and Warren, S. (2000). Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. *Journal of Experimental Marine Biology and Ecology*, **244:** 107-129.

Skov, Skov, M., Vannini, Vannini, M., Shunula, Shunula, J., Hartnoll, Hartnoll, R., Cannicci and Cannicci, S. (2002). Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae. *Marine Biology*, **141:** 725-732.

Skov, M. W. and Hartnoll, R. G. (2001). Comparative suitability of binocular observation, burrow counting and excavation for the quantification of the mangrove fiddler crab Uca annulipes (H. Milne Edwards). *Hydrobiologia*, **449:** 201-212.

Smith III, T. J. (1992). Forest structure, *In* Robertson, A. I. and Alongi, D. M. [eds.], *Tropical Mangrove Ecosystems. Coastal and Estuarine Studies*. American Geophysical Union. pp. 101-136.

Smith III, T. J., Boto, K. G., Frusher, S. D. and Giddins, R. L. (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.

Snedaker, S. C. (1995). Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. *Hydrobiologia*, **295:** 43-49.

Sotomayor, D., Corredor, J. and Morell, J. (1994). Methane flux from mangrove sediments along the Southwestern coast of Puerto Rico. *Estuaries and Coasts*, **17:** 140-147.

Spalding, M., Kainuma, M. and Collins, L. [eds.]. (2010). *World atlas of mangroves*. Earthscan. xv + 319 p.

Sukardjo, S. (1987). Natural regeneration status of commercial mangrove species (*Rhizophora apiculata* and *Bruguiera gymnorrhiza*) in the mangrove forest of Tanjung Bungin, Banyuasin District, South Sumatra. *Forest Ecology and Management*, **20:** 233-252.

Sweetman, A. K., Middelburg, J. J., Berle, A. M., Bernardino, A. F., Schander, C., Demopoulos, A. W. J. and Smith, C. R. (2010). Impacts of exotic mangrove forests and mangrove deforestation on carbon remineralization and ecosystem functioning in marine sediments. *Biogeosciences*, **7:** 2129-2145.

Tack, J. F. and Polk, P. (1999). The influence of tropical catchments upon coastal zone: Modelling the links between groundwater and mangrove losses in Kenya, India and Florida, *In* Harper, D. and Brown, T. [eds.], *Sustainable Management in Tropical Catchments*. John Willey and sons Ltd. pp. 359-372.

Tamooh, F., Huxham, M., Karachi, M., Mencuccini, M., Kairo, J. G. and Kirui, B. (2008). Below-ground root yield and distribution in natural and replanted mangrove forests at Gazi bay, Kenya. *Forest Ecology and Management*, **256:** 1290-1297.

Taylor, M., Ravilious, C. and Green, E. P. (2003). *Mangroves of East Africa*. UNEP World Conservation Monitoring Centre, Cambridge, U.K. 25 p.

Thom, B. G. (1967). Mangrove ecology and deltaic geomorphology, Tabasco, Mexico. *Journal of Ecology*, **55:** 301-343.

Thom, B. G. (1982). Mangrove ecology - a geormophological perspective, *In* Clough, B. [ed.], *Mangrove ecosystems in Australia*. Australian National University Press. pp. 3-17.

Tomlinson, C. B. (1986). *The Botany of Mangroves*. Cambridge University Press, Cambridge. 419 p.

Trumbore, S. (2006). Carbon respired by terrestrial ecosystems − recent progress and challenges. *Global Change Biology*, **12:** 141-153.

Trumbore, S., Costa, E. S. D., Nepstad, D. C., Camargo, P. B. D., Martinelli, L. A., Ray, D., Restom, T. and Silver, W. (2006). Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology*, **12:** 217-229.

Trumper, K., Bertzky, M., Dickson, B., van der Heijden, G., Jenkins, M. and Manning, P. J. (2009). The Natural Fix? The role of ecosystems in climate mitigation. A UNEP rapid response assessment, United Nations Environment Programme, UNEPWCMC, Cambridge, UK. 68 p.

Twilley, R. R. (1995). Properties of mangrove ecosystems related to energy signatures of coastal environments, *In* Hall, C. A. S. [ed.], *Maximum Power*. University of Colorado Press. pp. pp 43-62.

Twilley, R. R., Chen, R. H. and Hargis, T. (1992). Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air, & Soil Pollution*, **64:** 265-288.

Twilley, R. R. and Rivera-Monroy, V. H. (2005). Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research***:** 79-93.

UNEP (United Nations Environment Program). (1998). Eastern Africa Atlas of Coastal Resources 1: Kenya. (EAF-14) UNEP, 119 p.

UNEP (United Nations Environmental Program). (2001). The East African Coastal Resources Atlas 1: Kenya. ,

Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C., Moors, E. J., Granier, A., Gross, P., Jensen, N. O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A. S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Gumundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S. and Jarvis, P. G. (2000). Respiration as the main determinant of carbon balance in European forests. *Nature*, **404:** 861-865.

Valiela, I., Bowen, J. L. and York, J. K. (2001). Mangrove forests: one of the world's threatened major tropical environments. *BioScience*, **51:** 807-815.

Valiela, I., Kinney, E., Culbertson, J., Peacock, E. and Smith, S. (2009). Global losses of mangroves and salt marshes, *In* Duarte, C. M. [ed.], *Global Loss of Coastal Habitats: Rates, Causes and Consequences*. Fundacion BBVA. pp. 107-133.

van der Werf, G. R., Morton, D. C., DeFries, R. S., Olivier, J. G. J., Kasibhatla, P. S., Jackson, R. B., Collatz, G. J. and Randerson, J. T. (2009). CO_2 emissions from forest loss. *Nature Geoscience*, **2:** 737-738.

Van Speybroeck, D. (1992). Regeneration strategy of mangroves along the Kenya coast: a first approach. *Hydrobiologia*, **247:** 243-251.

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

Walters, B. B. (2005). Patterns of local wood use and cutting of Philippine mangrove forests. *Economic Botany*, **59:** 66 - 76.

Walters, B. B. (2008). Mangrove forests and human security. *CAB Reviews: Perspectives in in Agriculture, Veterinary Science, Nutrition and Natural Resources*, **3:** 1-9.

Warwick, R. M. and Clarke, K. R. (1993). Comparing the severity of disturbance: a metaanalysis of marine macrobenthic community data. *Marine Ecology Progress Series*, **92:** 221-232.

Wass, P. [ed.]. (1995). *Kenya's Indigenous Forests: Status, Management and Conservation*. IUCN. Xii + 250 pp. 252-8317-0292-8315

Xu, M., DeBiase, T. A., Qi, Y., Goldstein, A. and Liu, Z. (2001). Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. *Tree Physiology*, **21:** 309-318.

Ye, Y., Tam, N. F. Y., Wong, Y. S. and Lu, C. Y. (2003). Growth and physiological responses of two mangrove species (Bruguiera gymnorrhiza and Kandelia candel) to waterlogging. *Environmental and Experimental Botany*, **49:** 209-221.

APPENDICES

7.1 Appendix 1. Gas flux datasets for *R. mucronata* forest at Gazi bay, Kenya: values are mean for each sampling point

Date of treatment	Date	Period	Days	Treatment	Tempt (^{o}C)	Crab Burrows	$\mu mol CO_2$ m^{-2} s^{-1}	$nanmol CH_4$ m^{-2} s^{-1}
	June 9, 2009	Baseline	0			8	1.5	2.3
	June 24, 2009	Baseline	15		24.9	7	2.7	6.2
	July 8, 2009	Baseline	28		25.2	10	1.8	3.5
	July 23, 2009	Baseline	42		25.0	11	1.4	2.5
	August 10, 2009	Baseline	59		28.5	7	3.6	4.0
27th Oct to 2nd Nov 2009	Dec 2, 2009	Girdled	170	Control	30.2	8	4.0	7.6
	Dec 2, 2009	Girdled	170	**Treated**	**31.0**	**6**	**5.4**	**8.0**
	Jan 18, 2010	Girdled	225	Control	29.1	9	3.1	6.2
	Jan 18, 2010	Girdled	225	**Treated**	**29.9**	**7**	**3.6**	**10.6**
	March 4, 2010	Girdled	269	Control	30.9	10	3.1	5.4
	March 4, 2010	Girdled	269	**Treated**	**32.3**	**7**	**4.4**	**17.5**
	March 31, 2010	Girdled	294	Control	29.4	12	2.4	5.8
	March 31, 2010	Girdled	294	**Treated**	**30.6**	**9**	**3.7**	**10.6**
	April 28, 2010	Girdled	322	Control	28.6	8	2.4	5.0
	April 28, 2010	Girdled	322	**Treated**	**30.8**	**8**	**3.0**	**9.6**
5th-10th May 2010	May 28, 2010	Cut	350	Control	27.0	8	2.4	8.5
	May 28, 2010	Cut	350	**Treated**	**30.1**	**5**	**2.2**	**10.2**
	July 29, 2010	Cut	412	Control	26.2	11	2.6	9.7
	July 29, 2010	Cut	412	**Treated**	**29.8**	**10**	**2.8**	**7.0**
	Sept 8, 2010	Cut	452	Control	26.1	10	2.5	3.3
	Sept 8, 2010	Cut	452	**Treated**	**29.0**	**9**	**3.2**	**3.8**
	Nov 7, 2010	Cut	510	Control	29.9	10	2.1	4.8
	Nov 7, 2010	Cut	510	**Treated**	**35.7**	**12**	**5.6**	**5.8**
	Jan 23, 2011	Cut	586	Control	29.4	9	4.1	9.6
	Jan 23, 2011	Cut	586	**Treated**	**33.2**	**11**	**3.7**	**6.9**
	March 7, 2011	Cut	628	Control	30.6	9	4.3	10.0
	March 7, 2011	Cut	628	**Treated**	**35.2**	**11**	**4.6**	**3.7**
	April 18, 2011	Cut	669	Control	31.0	7	3.7	7.5
	April 18, 2011	Cut	669	**Treated**	**35.1**	**5**	**3.0**	**1.9**

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7.2 Appendix 2. Aboveground production datasets for the four mangrove forest types at Gazi bay, Kenya: DBH = stem diameter, Ht = tree height, BA = basal area, AGB = aboveground biomass and GBH = girth at breast height.

Site	Forest	Plot (100 m^2)	Stems	DBH (cm)	Tree Ht (m)	BA (m^2)	AGB (kg)	GBH Increment (mm yr^{-1}) Dendro	Circum
Gazi	*Avicennia*	1	53	4.2	3.8	0.08	273.3	-	5.6
		2	48	3.5	3.0	0.05	144.1	-	7.4
		3	57	4.2	3.7	0.09	298.6	-	7.4
		4	35	8.9	6.4	0.27	1121.4	-	5.8
		5	31	8.2	5.7	0.19	725.1	-	6.0
		6	34	8.4	7.6	0.23	1103.6	-	7.4
	Ceriops	1	48	3.9	2.8	0.10	148.1	-	10.8
		2	69	2.9	2.4	0.05	135.3	-	8.3
		3	37	2.9	2.0	0.03	70.8	-	4.8
	Rhizophora	1	42	4.9	5.0	0.13	1191.9	-	15.7
		2	47	4.8	4.6	0.15	1181.8	-	14.3
		3	34	4.2	4.9	0.06	555.4	-	16.3
		4	42	5.9	6.0	0.17	1951.5	-	11.6
		5	46	4.5	4.9	0.10	769.5	-	13.7
		6	33	7.6	5.6	0.21	1721.5	-	12.5
	Sonneratia	1	39	5.1	4.2		376.9	-	25.1
		2	36	11.4	7.3		1797.3	-	25.8
		3	34	9.6	6.8		1212.6	-	21.3
Makongeni	*Avicennia*	1	31	7.2	5.1	0.15	585.3	7.0	16.3
		2	26	6.7	4.8	0.11	404.1	4.2	12.9
		3	35	7.2	4.7	0.17	605.2	3.1	16.1
		4	29	6.3	5.4	0.13	550.8	7.5	14.1
		5	33	6.7	5.5	0.18	747.5	3.1	9.1
	Rhizophora	1	39	4.9	5.2	0.13	956.0	12.5	17.3
		2	42	6.0	6.1	0.16	1140.8	26.3	13.5
		3	44	5.7	5.6	0.22	1972.1	6.1	13.0
		4	61	5.1	5.2	0.18	1232.2	15.3	20.3
		5	47	5.6	5.5	0.16	984.2	12.5	32.6