INFLUENCE OF SPECIES DIVERSITY ON THE RETURN OF ECOSYSTEM FUNCTIONS IN REPLANTED MANGROVES IN KENYA

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Thesis

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DEDICATION

This thesis represents the pinnacle in long road of academic endeavour. It is a rewarding product to my parents for the long and sometimes difficult moments that has witnessed a remarkably amazing acts of sacrifice, tenacity, resolve, self denial and sometimes desperate measures all in the effort of ensuring I received this fundamental human right. To Joseph and Agnes thanks for the perfect eternal gift

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PREFACE

The global rate of mangrove degradation has been estimated at 1-2 % globally (FAO, 2003). In attempts to address the problem, several mangrove restoration initiatives have been formulated in many areas of the world. The aims of these reforestation programs varies but are generally centred on production forestry, sediment stabilization and enhancement of fisheries production. This study aimed to experimentally manipulate different combinations of mangrove species and to measure a range of ecosystem functions such as aboveground biomass production. This work is divided into six chapters:

Chapter One: Introduces the concepts of biodiversity and ecosystem goods and services, giving a plethora of biodiversity-ecosystem services experiments conducted in grasslands and terrestrial forest. Mangrove goods and services, biogeographical distribution, threats to mangroves as well as restoration efforts are explored. Aspects of mangrove growth performance including biomass increment and sediment CO_2 efflux are also discussed.

Chapter Two: Provides an insight into the sapling survival status in the mixed species plots as well as in a monoculture *Sonneratia* plantation established in 2003. Findings in this chapter point to difference amongst the planted species in tolerance to sediment salinity as the key determinant of survivorship among the planted species. *Avicennia marina*, given its wide tolerance range to salinity levels has the highest survival rates (87 %) followed by *Ceriops tagal* (71%) and finally *Bruguiera gymnorrhiza* (29%). Location of the tree and size of the sapling

at planting did not influence sapling survival at both sites. Species richness also had no influence on sapling survival. It is the species traits that enable species to muster prevailing environmental conditions and ultimately its establishment and success. Also prior existence of a species in reforestation site does not guarantee its immediate successful established given that due to long term exposure, the sediment undergo shifts in its physico-chemical characteristics rendering it unsuitable for the establishment of the species previous located there.

Anthropogenic impacts on biodiversity across a wide range of ecosystems are now well documented; however the responses of ecosystems to reduced diversity are still poorly understood. **Chapter Three** investigates the effects of species richness, species identity and environmental variables on aboveground biomass and natural recruitment I replanted mangroves. Results indicate that whereas harsh site conditions slowed growth considerably in the first two years, significant species richness effects on aboveground biomass was observed in the third year (2007). *Avicennia marina* exhibited strong competitive and 'nursing' traits, for instance it had the best growth rate, and also it enhance the growth of other species when planted in mixtures. Partitioning of net effects showed strong species selection effect but complementarity effects were exhibited in some of the three species plots. Aboveground biomass was positively correlated with height above sea level, whilst sediment salinity, ammonium and phosphate concentration were negatively correlated with height above sea level. A facilitation effect was observed in the recruitment of wild

plants, with *Avicennia* acting as a 'nursery species' for recruits of other species, particularly *Ceriops tagal*.

Chapter Four reports on belowground root distribution and production. Belowground biomass component has the potential to contribute to mitigation of atmospheric carbon dioxide given it constitute between 15-55 % of total biomass in mangrove (Alongi, 2002). However what is less understood is the extent of influence of species traits, stand structure and composition as well as environmental controls on this hidden component of total biomass. Findings here show that species richness and sediment depth significantly influenced root biomass. Also comparisons of *Avicenna* root biomass from this stand with a 12 year plantation and a naturally growing stand are made. The stand root: shoot ratio was also influences by species richness. Root biomass was positively correlated with soil nitrate, % silt and negatively correlated with salinity and ammonium. *Avicennia marina* exhibited strong growth characteristics exerting its effects on root distribution at different mixed species plots as well as at different sediment depths.

Increasing atmospheric carbon dioxide concentrations and declining species diversity are some of major global change problems caused by human activities. **Chapter Five** measured temporal variation in soil CO_2 efflux and the influence of species richness, temperature and soil moisture content Results indicate significant effects of tidal period and soil temperature on soil CO_2 efflux. Other factors i.e. species richness, soil moisture and year did not significantly affect soil CO_2 efflux. Increasing soil CO_2 efflux exhibited a temporal pattern which was clearly related to soil temperature pattern. Also there was higher soil CO_2 efflux immediately after spring tides compared to in the middle of neap tide. Given the observed pattern of increasing fluxes with time, it is anticipated that considerable contribution from planted trees as well as from increased microbial diversity arising from changes in sediment micro-climate will become profound with time. Also it is envisaged that species richness effect will become apparent as the trees mature.

Finally **Chapter Six** provide a synthesis of the preceding chapter setting the study in the context of the current themes in biodiversity-ecosystem function debate as well as defining limitations of the study. Finally recommendations are made including need for further work on several issues arising from this study.

TABLE OF CONTENTS

5.0 CHAPTER 5. TEMPORAL DYNAMICS OF SOIL CARBON DIOXIDE EFFLUX IN A RESTORED YOUNG MANGROVE PLANTATION AT GAZI BAY KENYA 110

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Rates of loss of biodiversity caused by human action are on the increase worldwide. However implications of species loss on the natures' ability to provide ecosystem services and goods are still poorly understood. Despite providing an array of critical services and goods, mangrove ecosystems are under intense threat. In attempts to address the problem, several mangrove restoration initiatives have been formulated in many areas of the world with different objectives. Over the last two decades, experiments manipulating species diversity and measuring ecosystem functions have been conducted mainly using grassland ecosystems and have exhibited positive relationships. More recently, experiments investigating this relationship have emerged in long-term woody species i.e. trees; however these have concentrated on terrestrial forests. This study experimentally manipulated different mangrove species and measured a range of ecosystem functions including sapling survival, above and belowground biomass production and sediment CO_2 efflux.

Enhanced sapling growth was positively correlated with plot height above datum, percentage silt and nitrates and negatively correlated with sediment salinity, ammonium and phosphates. Also high values of above and belowground biomass, root: shoot ratios, mean tree height, leaf area index as well as naturally recruited saplings were observed in mixed plots (particularly with *Avicennia marina* in the mixture) compared with monospecific plots. Species selection effect, particularly from the fast growing *A. marina* species was the mechanism behind a range of the observed ecosystem functions.

However complementarily effects were observed particularly on aboveground biomass. However sapling survival and sediment CO_2 efflux was not influenced by species richness. We conclude that there is variation in the stages of plant development at which species richness effects manifest themselves, in addition the effects of environmental variables has a bearing on the nature and direction of the relationship between species richness and ecosystem function. We anticipate changes in the plots structure over time from *Avicennia* facilitative effects which are expected to lead to changes in sediment microclimate inducing changes in other species growth and promoting recruitment and development of wildlings.

CHAPTER 1: INTRODUCTION

1.1 Ecosystem Goods and Services

Societies rely on natural ecosystems to derive essential goods (Constanza et al., 1997; Daily, 1997; Brauman et al., 2007). These goods include seafood, timber, game animals, fodder, biomass fuels, natural fibre, animal products and pharmaceutical products many of which are commonly traded in economic markets. The annual world fish catch, for example, amounts to about 100 million metric tons and is valued at between $50 billion and $100 billion; it is the leading source of animal protein with over 20% of the population in Africa and Asia alone depending on fish as their primary source of protein (FAO, 1994).

What has been less appreciated until recently is that natural ecosystems also provide services without which human civilizations would cease to thrive (Turner and Daily, 2008). These ecosystem services are the processes and conditions of natural ecosystems and species that make them up that support human activity and sustain human life (Daily, 1997) examples include flood protection climate regulation, oxygen production, soil formation and aesthetic values The concept of ecosystem services is a more recent development and is receiving growing attention (Mooney and Ehrlich, 1997; Eamus, 2005). Its main virtue is that it allows the integrated analysis of ecological and social aspects of ecosystem management as well as environmental issues (De Groot et al., 2002). It is also an excellent concept to inform stakeholders and policy makers about human dependence on ecosystems and the need to put in place strategies that ensures sustainable management of resources (Turner et al., 1998; Daily et al., 2000).

Human activities are impacting negatively on nature's ability to provide ecosystem services (Vitousek et al., 1997; Daily, 1997; Millennium Ecosystem Assessment, 2005; Constanza et al., 2007). Foremost among the immediate threats are habitat modifications and destruction, overexploitation and increased rates of invasions by non-native species (Naeem et al., 1999; Millennium Ecosystem Assessment, 2005; Turner and Daily, 2008). A conservative estimate of the rate of species loss is ~8,000 per annum, which unfortunately exceeds the rate of evolution of new species by a factor of 10,000 or more (Wilson, 1989; Lawton and May, 1995). But complete loss of species is only the final act in the process. The speed of loss of local populations of species - the populations that generate ecosystem services in specific localities and regions - is thought to be much higher (Daily and Ehrlich, 1996; Yuan-Farrell, 2006).

The threats to ecosystem services come from rapid, unsustainable growth in the scale of the human enterprise, in population size and per-capita consumption, and also in the environmental impacts that technologies and institutions generate as they produce and supply these consumables (Ehrlich et al., 1977; Metzger et al., 2006). Ecosystem services are generally greatly undervalued, for a number of reasons: many are not traded or valued in the marketplace; many serve the public good rather than provide direct benefits to individuals; landowners often have no way to benefit financially from the ecosystem services supplied to society by their land; and also, economic incentives often encourage the conversion of lands to other, market-valued activities. Thus, people whose activities disrupt ecosystem services often do not pay directly for the cost of those lost services. Also, society often does not compensate landowners and others who do safeguard ecosystem services for the economic benefits they lose by foregoing more lucrative but destructive land use (Daily, 1997).

1.2 Biodiversity and Ecosystem Function Relationships

Biodiversity and ecosystem functions are broad concepts potentially linked at different scales (Field et al., 1998). The term biodiversity is a contraction of biological diversity and came into usage after the signing of the Biodiversity Convention at the United Nations Conference on Environment and Development in Rio in 1992. The Convention defined biodiversity as *'the variability among living organism from all sources including inter alia terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this include diversity within species, between species and of ecosystems'.* It is described, quantified, managed and used at various scales from genotypic diversity within a population, through population diversity within a species, and species diversity within ecosystems (Jermy et al., 1995; Field, 1998) While genotypic diversity experiments are a relatively newer field, various aspects of biodiversity have been addressed at species level experiments e.g. in grasslands (Naeem et al, 1994; Tilman and Downing, 1994) freshwater ecosystems (Hooper et al., 2005) shallow coastal waters (Emmerson and Huxham, 2003; Raffaelli et al., 2003; Allison, 2004) and trees (Scherer-Lorenzen et al., 2007).

Ecosystem functions refer to the system properties or processes occurring within and between ecosystems, such as nutrient recycling (Costanza, 1997). It differs from ecosystem services in that it refers to system processes and properties that are not necessarily of immediate benefit to man. Field et al. (1998) describes ecosystem functions in terms of fluxes of energy and matter and the structural and physical elements of ecosystems and categorizes the functions to cover three major areas i.e. biogeochemical, ecological and anthropocentric with overlaps between (Figure 1.1). In the ecosystem function-biodiversity debate, two types of function are commonly considered: productivity of the system e.g. biomass, nitrogen fluxes; and stability of the system e.g. resilience and resistance (Lawton et al., 1994).

Biodiversity is considered to be important for a variety of reasons (see UNESCO, 1994). Recent attention has focused on its potential importance for the adequate functioning of the earth's ecosystems (Schulze and Mooney, 1993). The interest in this issue has grown from concerns about the potential ecological consequences of the present and projected future loss of biodiversity caused by the increased impact of human activities on natural and managed ecosystems. There has been growing recognition that ecosystems operate in a manner that provides ecological goods and services to humans, the economic significance of which might be considerable (Costanza et al., 1997). These services are derived from the normal functioning of ecosystems thereby raising the important question whether depauperate ecosystems perform differently or less efficiently than the more species-rich systems from which they are derived (Schulze and Mooney, 1993; Chapin III et al., 2001).

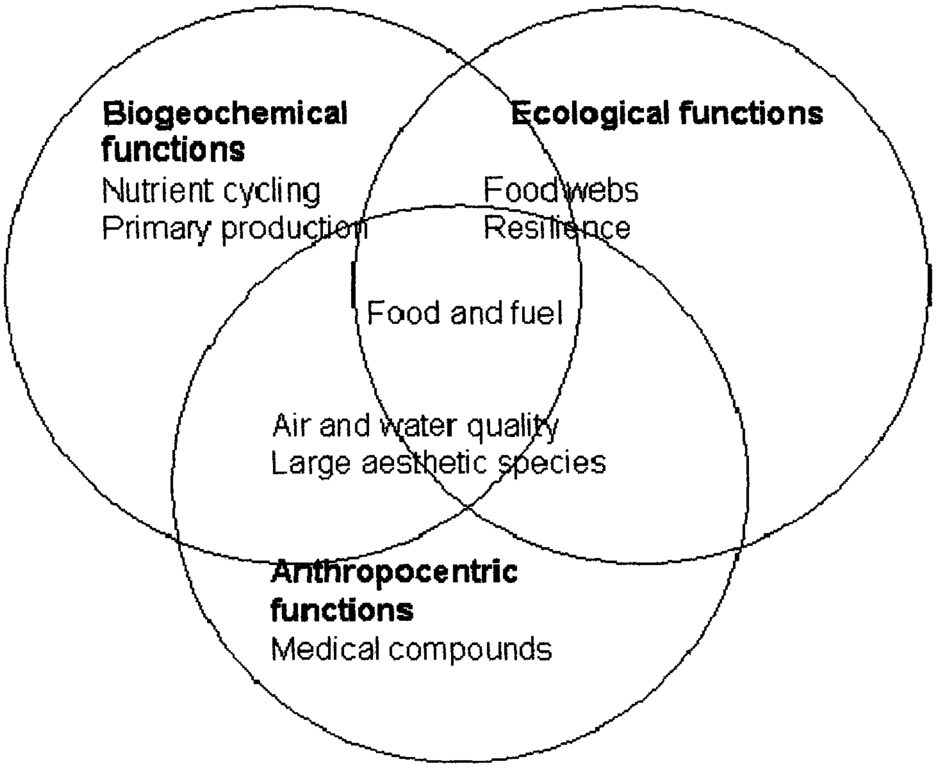

Figure 1.1: Overlaps in various categories of ecosystem functions (Redrawn from: Field et al., 1998)

In attempts to fully understand the nature of the biodiversity and ecosystem function relationship, heuristic models have been proposed as ways in which ecosystem functions could respond to species loss. Naeem et al. (2002) proposed four main hypotheses (Figure 1.2). First, the redundant species hypothesis suggests that many species perform the same function and reduction of species number does not alter the ecosystem function (although many may provide "insurance" against future disturbances). However, this hypothesis suggests that there is a minimum diversity necessary for proper ecosystem function. Second, the rivet hypothesis suggests that all species have singular important contribution to ecosystem performance. This hypothesis likens species to rivets holding a complex machine, and postulates that functioning will be impaired as rivets (species) fall out. Third, the idiosyncratic response hypothesis suggests that species impacts are context-driven and ecosystem function changes when diversity changes, but the magnitude and direction of change is unpredictable because the roles of individual species are complex. Fourth, the null hypothesis proposes that ecosystem function is insensitive to any changes in diversity.

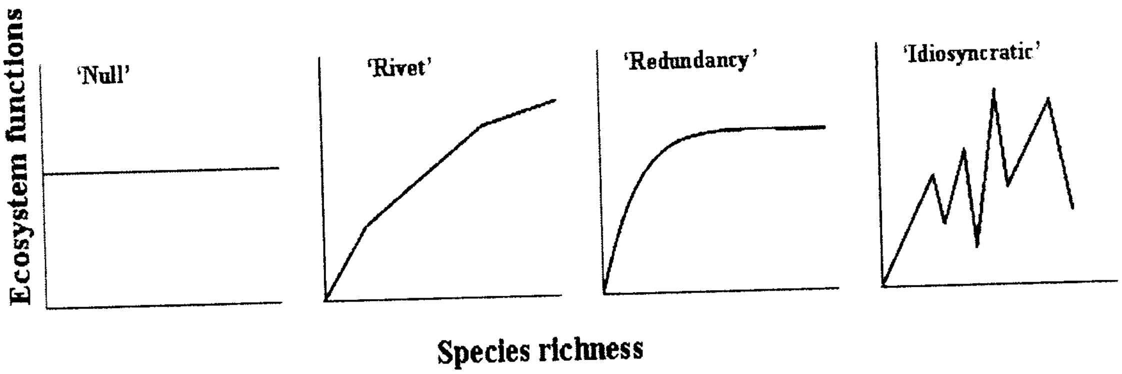

Figure 1.2: Conceptual models relating biodiversity to ecosystem functions (Redrawn from: Huxham and Sumner, 2000)

1.2.1 Experimental approach

1.2.1.1 Short-term experiments

In the last decade, ecologists in testing these contrasting hypotheses have investigated the relationship between diversity and function using manipulative experiments initially in grassland ecosystems and more recently on other ecosystems (e.g. Naeem et al., 1994; Emerson and Huxham, 2002; Allison, 2004; Hooper et al., 2005). The initial experiment was conducted in a controlled environmental facility designed for ecological research (Naeem et al., 1994). It established replicates of high, intermediate and low diversity, grassland ecosystems. In a combinatorial design, it established 164 combinations of the 16 species of grass used in the main experiments at constant densities (Naeem et al., 1996). The study established that the relationship between diversity and ecosystem functioning was not flat and attributed the positive relationship between species diversity and production to existence of species complimentarity. However, the study design could not address many issues that would emerge as biodiversity-functioning research evolved (Lawton et al., 1998).

Two experimental studies initiated in 1994 contributed immensely to biodiversity-ecosystem function research (Tilman et al., 1997). The first of these consisted of smaller plots (3m × 3m) planted with 7 levels of gradients of biodiversity of plant species. The composition of each plot was determined by a separate random draw from a pool of 24 species. The second study was similar except the plots were 9 m x 9 m and 5 levels of gradients of species diversity randomly chosen from a pool of 18 species. The two experiments showed positive correlations between the number of species planted and plant biomass and negative correlations with the levels of unconsumed soil nitrate. However, they also showed that functional group composition of plots was as important as species richness in controlling these measures of ecosystem functioning (Tilman et al., 1997).

These results and those from a multiple-site experiment (Hector et al., 1999) stimulated vigorous debate regarding the mechanism behind the biodiversity-ecosystem function relationship. Were these results caused by sampling effects, resulting from the higher probability that more diverse plots would contain and become dominated by a highly productive species? or were they caused by complementarity effects, that is, did the differences in the ecological niches of species lead to more complete use of resources in more diverse plots (e.g., Huston 1997; Wardle, 1999; Huston et al., 2000)? Results from the Cedar Creek experiment (Tilman et al., 1997) suggested that both mechanisms were responsible for the positive relationships found between diversity and ecosystem functioning, with species selection effects explaining much of the correlation early in the experiment (1 to 3 years) but longer-term results (5 to 6 years) being more consistent with the mechanism of complementarity (Tilman et al., 2001). This trend persists in a more recent study by Fargione et al. (2007).

A synthetic community experiment addressed the questions about how diversity loss interacted with other aspects of global change (Reich et al., 2001). In this experiment, plant diversity was manipulated in combination with atmospheric carbon dioxide (CO_2) and nitrogen (N) deposition in small plots. The results of the first 2 years confirmed the diversity–biomass and diversity–soil nitrate relationships found in the previous experiments. In addition, biomass accumulation in response to elevated CO_2 or N was greater in species-rich than in species-poor plots, both because the more diverse plots were more likely to contain dominant species (sampling effect) and because of niche differentiation (complementarity effect) (Reich et al., 2001).

1.2.1.2 Long-term forestry experiments

Most of the manipulative biodiversity experiments initiated so far have used fast-growing and small-model systems e.g. grasslands and aquatic or terrestrial microcosms. Woody species have been excluded from these early experiments despite the ecological and socio-economic importance of the forest ecosystems (Scherer-Lorenzen et al., 2007). The big question whether the relationships and their underlying mechanisms observed at these systems exist in forests still remains unanswered. However, forestry science is replete with a large body of knowledge about the effects of mixing species dating back to the 18th century (Pretzsch, 2005). Recent reviews have inferred the presence of niche partitioning and facilitation in certain types of mixed forests (Cannell et al., 1992; Pretzsch, 2005) for instance, combinations of sun-adapted species in the over storey and shade-adapted species in the under storey as well as mixtures with different rooting systems fall into these categories (Scherer-Lorenzen et al., 2007)

In studying the connection between tree diversity and ecosystem function, it is necessary to establish a gradient in the species ranging from single species to multiple mixtures (Scherer-Lorenzen et al., 2005). There are two approaches adopted in creating this species gradient. First, pre-existing stands can be subjected to "removal experiments" where species are removed from an already established multi-species stand or to "addition experiments" where species are added to an already existing monostand and/or low-diversity. Second, entirely new forest stands with different number of species can be established; this is called the "synthetic-community approach" which is the approach adopted by the recently established, long-term experiments examining the role of tree diversity on ecosystem functions (see Table 1.1). One notable feature of these experiments is their terrestrial location and the use of terrestrial trees.

To my knowledge no manipulative experiments testing effects of diversity on ecosystem functions in mangroves have been conducted. This is despite the fact that compared to terrestrial forests where species diversity levels of up to 250 have been recorded in tropical rainforests (Anthony and Woodruff, 1980), mangroves offer the advantage of relatively low natural species richness; for instance, complete functioning communities often has about two species and rarely over five species at a local scale of meters to hectares (Osborn and

Polsenberg, 1996) thereby making it possible to possible include all the species without necessarily requiring to have large sets of species treatments.

Table 1.1: Global tree diversity experiments

Biome	Country	Planting	No of sites	Plot size	Total no of plots	Diversity variables	Diversity gradients	Size of species pool
Boreal	Finland	1999	3	0.04 ha	114	Species richness	1, 2, 3,5 species	5
						Number of functional groups	Deciduous /coniferous	
Boreal	Finland	2000	1	0.004 ha	49	Genetic diversity of *B. pendula*	1,2,4, 8 clones	8 clones
Temperate	Germany	2003/04	2	1.2 ha	40	Species richness	1,2,4,6 species	6
				0.6 ha	16	Species richness	1,2,3,4 species	4
Temperate	Germany	2003	1	0.2 ha	25	Functional diversity of 4 species mixtures	Continuous	16
Tropical	Panama	2001	1	0.2 ha	24	Species richness	1,3,6 species	6
						Identity of functional groups	Pioneer, shade-tolerant,	
Tropical	Panama	2003	1	0.03 ha	24	Species richness	6,9,18 species	28
						Assemblage identity	4 different assemblages	
Tropical	Panama	2002/3	1	4.0 ha	124	Species richness	1,4, 16 species	16
						No. of genera	2 vs 4 genera	
						Tree height	2 vs 3 height classes	

Source: Scherer-Lorenzen et al., 2005

1.3 Mangrove Ecology

Mangrove ecosystems or 'mangals' (MacNae, 1968) occur worldwide along sheltered tropical and sub tropical coasts between latitudes 30°N and 30°S of the equator (Spalding et al., 1997) and consist of a diverse association of woody trees and shrubs that form dominant vegetation in tidal, saline wetlands (Chapman, 1976; Tomlinson, 1986). In Kenya, mangroves are found in creeks, bays and estuaries and estimates of total area under mangrove vary according to different sources. The Kenya Forest Department estimates coverage of 644 km^2 while the World mangrove Atlas estimate is 961 km^2 (Spalding et al., 1997). However, a more rigorous study made by Doute et al. (1981) indicated that there were 531 km^2 of mangroves in Kenya the bulk of which were in Lamu District (335 km^2) and substantially smaller areas in Kwale (88 km^2) and Mombasa Districts (20 km^2). There are nine mangrove species belonging to six families in Kenya (Gallin et al., 1989; Kairo, 2001).

Mangrove ecosystems are heterogeneous habitats with an unusual variety of animals and plants adapted to the environmental conditions of highly saline, frequently inundated, soft bottomed anaerobic mud (Hogarth, 1999). To survive in these conditions, mangroves have developed morphological and physiological specializations notably; aerial breathing roots; support roots and buttresses; high salt tolerance; salt secreting leaves and viviparous water dispersed propagules (Walsh, 1974; Tomlinson, 1986; Hogarth, 1999: Dahdouh-Guebas, 2007). The mangrove fauna includes terrestrial, marine, incidental and resident animal species, all of which have different adaptations to cope with the mangrove environment (Hogarth, 1999).

1.3.1 Mangrove ecosystem goods and services

Mangroves supply a variety of ecosystem goods. Directly produced goods include raw materials such as wood (also used as a fuel), leaves, *Nipa* shingles and tannins crabs, and resources for traditional medicines (Dahdouh-Guebas et al., 2000; Abuodha and Kairo, 2001; Kairo et al., 2002). Offshore fish and shellfish which use the mangrove ecosystem as a nursery comprise indirectly-produced goods (Mumby et al., 2004).

Mangrove ecosystems also provide ecosystem services (Ewel et al., 1998). Mangrove areas are primary nursery areas for commercially important species of fish (e.g. Christensen, 1978; Kimani et al., 1996) and contribute to offshore productivity via the outwelling of detritus (Odum and Heald, 1975). Mangroves are located in sediments which are frequently waterlogged and anoxic. The problem of supplying air to the roots is solved by above-ground root systems which, in turn, determine the physical structure of this ecosystem (Hogarth, 1999). The root systems retard water flow and create a quiet environment that encourages sedimentation and inhibits resuspension (Field, 1995). This encourages sediment stabilization which leads to shoreline protection (Wolanski et al., 1992; Young and Harvey, 1996). Mangrove ecosystems can function as a sink for dissolved and suspended substances removed from through-flowing water by sedimentation as well as uptake by organisms attached to the roots (Wolanski, 1991; Walsh, 2004). Mangroves also perform waste disposal services by removing fertilizer and pesticide surpluses, industrial wastes and sewage (Levin et al., 2001). Fixation of carbon dioxide is also identified as a service by mangroves (Ong, 1993; Alongi, 1999; Cebrian, 2002). Indirect interest in species found in mangrove ecosystems stems from an appreciation of the diversity of life and/or individual species (ecotourism). Mangroves also provide services that are associated with knowledge, e.g. many mangroves are visited by students and scientists. Key ecological processes associated with these environmental functions are summarized in Figure 1.3 below.

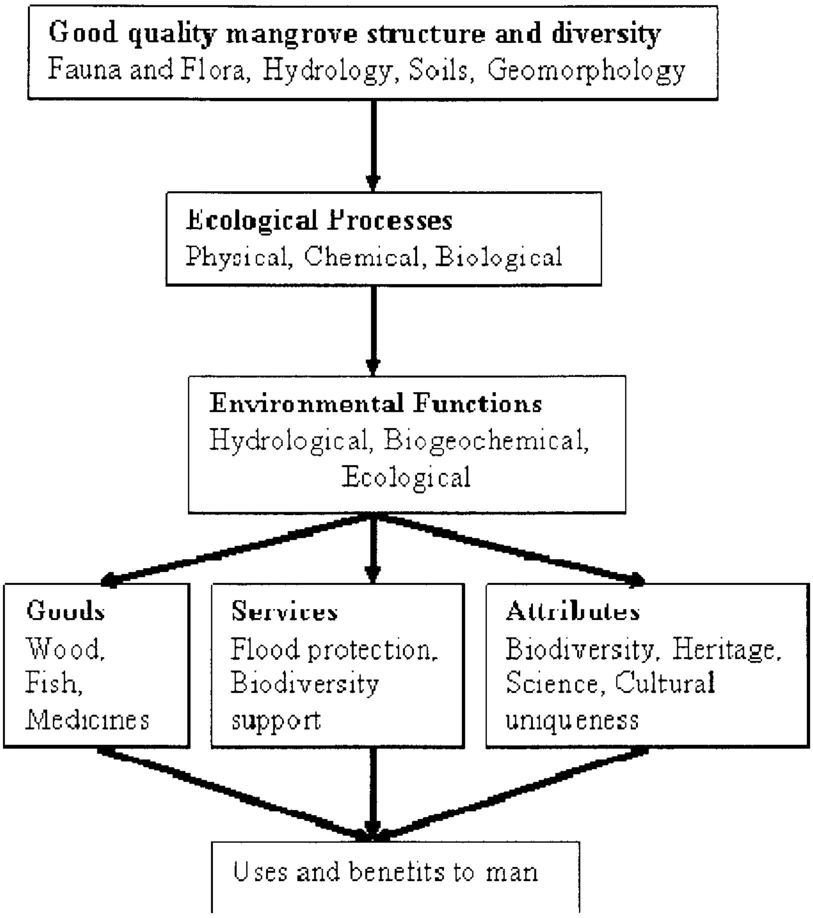

Figure 1.3: Links between mangrove diversity and supply of goods and services useful to man (Redrawn from: Gilbert and Jansen, 1998)

1.3.2 Mangrove biogeography

Mangrove ecosystems are estimated to cover 181,000 km^2 worldwide (Spalding et al., 1997). Approximately 112 countries have mangrove resources within their borders. Some of the largest mangrove areas are found in Indonesia (42,550 km^2), Australia (11,500 km^2), Brazil (13,400 km^2) and Nigeria (10,515 km^2). Mangroves in Kenya are estimated to cover 54,000 hectares (Doute et al., 1981). The global distribution of mangroves can be divided into two hemispheres, the Atlantic East Pacific (AEP), commonly referred to as the New World and the Indo West Pacific (IWP) referred to as Old World (Duke, 1992). Species diversity is highest in the IWP region and decreases westwards with minimal species in the West Africa region. Under this classification, the Eastern Africa mangroves fall under the IWP mangroves and comprise ten species compared to South East Asia mangroves whose species diversity ranges up to fifty species (Tomlinson, 1986).

Mangroves are relatively species poor when compared to other high biomass tropical ecosystems like rain forests (Ricklefs and Latham, 1993). The harsh survival conditions pertaining in the intertidal areas where mangroves are located may be responsible for the low species diversity. However, despite comparatively low plant species diversity, the diversity of other life forms is much greater with high abundance of arthropods, molluscs, fish, and birds (Field, 1998). On a large land mass or within a group of islands, mangrove plant species diversity tends to increase with precipitation and area of watershed (Duke, 1992) and to decrease with increasing latitude (Saenger and Snedaker, 1993; Duke, 1998).

The diverse habitat variation is efficiently compressed into a compact range within a mangrove ecosystem. For instance, the gradient from full-strength (or sometimes hypersaline) seawater to freshwater spans the water range potential experienced by mangroves (Osborn and Polsenberg, 1996). The gradient from fully submerged to fully exposed sites further enhances the diversity of mangrove habitats (Field, 1988).

1.3.3 Threats to mangroves

Historical records indicate that the original extent of mangrove forests has declined considerably. National proportions of original mangrove cover lost vary from 4 to 84% with the most rapid losses occurring in recent decades (FAO, 2003; 2007). For example, in Southeast Asia Malaysia lost 12% from 1980 to 1990 (Ong, 1995); Thailand had 5,500 km^2 in 1961 but 2,470 km^2 remained in 1986 (Aksornkoae, 1987) and Vietnam had an estimated 4,000 km^2 originally but had reduced by 37 % in 1997 (Spalding et al., 1997).

These losses have largely been attributed to anthropogenic pressures such as over-harvesting for timber and fuel-wood production (Semesi 1998; Hogarth 1999; Dahdouh-Guebas et al., 2004), reclamation for aquaculture and salt pond construction (Primavera, 1995), and mining, pollution and damming of rivers that alter water salinity levels (Wolanski, 1995). Oil spills have impacted mangroves dramatically in the Caribbean (Farnsworth and Ellison, 1997) but little documentation exists for other parts of the world. A major threat to mangrove wetlands is their conversion to areas of aquaculture. After the development of intensive shrimp farming techniques in Taiwan in the 1970's, there was a sudden rush into modern shrimp farming in Southeast Asia spreading to the

Caribbean and Latin America (Farnsworth and Ellison, 1997). In the Indo-Western Pacific region alone, 1.2 million hectares of mangroves had been converted to aquaculture ponds by 1991 (Primavera, 1995). In Eastern Africa, there are no up-to-date data available to give accurate pictures of the current condition of mangrove forests. However, various reports (e.g. Ferguson, 1993; Semesi, 1998; Abuodha and Kairo, 2001; FAO, 2003, 2007) have indicated that extensive bare lands resulting from indiscriminate cutting of the trees occur all over the region.

1.3.4 Mangrove reforestation initiatives

Increasing awareness of the value of mangroves has led to renewed efforts to protect and restore them. Mangrove planting and management has a long history in Southeast Asia (e.g. (Gan, 1993; Ong, 1995). Perhaps the longest recorded history of mangrove management for timber is in the Sundarbans. The 6,000 km^2 of mangrove forests that cover the Sundarbans region of India and Bangladesh, were managed since 1769 and detailed work-plans prepared in 1893-1894 (Chowdhury and Ahmed, 1994). A parallel example is given by the 40,000 ha mangroves of Matang (Malaysia) that have been managed for fuel-wood production since 1902 (Gan, 1993; Ong, 1995). The mangrove reforestation provides significant employment to the local people, and the use of mangrove wood products for timber and charcoal makes a significant contribution to the economy of the west coast Peninsular Malaysia (Chan, 1996).

More recently, mangroves have been managed for integrated fish culture and for eco-tourism (Primavera, 1995). Planting mangroves has also been applied for erosion control in Florida (Teas, 1977) and for experimental analysis of mangrove biology in Panama (Rabinowitz, 1978). In East Africa, information on earlier mangrove plantation practices is scanty. Only in Kenya is reference made to mangrove planting in Lamu, (Rawlins, 1957; Roberts and Ruara, 1967) and Gazi bay (Kairo, 1995, Kairo et al., 2001). Unfortunately, mangrove rehabilitation has often been carried out simply by planting mangrove seedlings without adequate site assessment, or subsequent evaluation of the success of planting at the ecosystem level (Kairo, 1995). Moreover, for economic and technical reasons, mangrove reforestation efforts are often limited to Rhizophoreceae. This raises obvious questions regarding habitat change and reduced ecological function in mangrove plantations compared to natural, mixed species mangrove stands.

In Kenya, research on mangrove forest restoration has a long history (e.g. Kairo, 1995) and the influence of mangrove trees on the adjacent ecosystems is well documented (Huxham et al., 2004; Crona and Ronnback, 2005). However, knowledge of the relationship between species diversity and ecosystem functioning is still weak and derives mainly from comparative observations of vegetative structure, faunal diversity between natural stands and replanted sites (e.g. Bosire et al., 2003). Environmental differences among these systems may obscure potential within-habitat effects of biological richness on ecosystem processes in such comparative studies (Loreau, 2004). Therefore, within-site biodiversity experiments manipulating species diversity while keeping other ecological factors as constant as possible are appropriate in complementing observational diversity-functions studies.

1.4 Mangrove Biomass

1.4.1 Aboveground biomass

Aboveground biomass components in mangroves consist of leaves, branches, stems, and in species such as *Rhizophora,* prop roots. Typically, leaves contribute 3 to 5 %, branches 10 to 20 % and the main trunk 60 to 90 % of total biomass, while aerial prop roots, where present, may amount to between 8 to 25 % of the total aboveground biomass (Clough and Scott, 1989). Total aboveground biomass varies widely in mangroves, typically it is highest at low latitudes and declines northward and southwards from the equator (Saenger and Snedaker, 1993). Some undisturbed *Rhizophora* forests in northern Australia may reach values of up to 700 tons dry weight per hectare (t ha^{-1}), but a range of 500 to 550 t ha^{-1} is more usual in old stands of mangrove forests of South East Asia. These values may be close to the maximum for natural undisturbed mangrove forest in warm humid tropics. When less favourable conditions such as lower temperatures, aridity, hypersaline soils, or nutrient limitation exist, aboveground biomass is usually somewhat less than these maximum values. For instance low values of 6.8 t ha^{-1} have been reported

(Saenger and Snedaker, 1993). In addition, major periodic events such as severe coastal storms or cyclones, soil erosion and soil accretion can also have significant impacts on the accumulation of above ground biomass by mangrove forests (Clough, 1992).

Aksornkoae et al. (1987) reported the biomass yields of various mangrove vegetation zones in Thailand. The *Rhizophora* zone was highest yielding 710.63 t/ ha^{-1} followed by *Bruguiera* zone (243.75 t/ ha^{-1}) and least was *Sonneratia* zone (128.75 t/ ha^{-1}). *Sonneratia* species are 'soft' species compared to *Rhizophora* and their dry weight may vary while standing crop may appear complex. Lower biomass in *B. gymnorrhiza* (62.5 t/ ha^{-1} and 94.49 t/ ha^{-1}) has been reported in Puerto Rico (Golley et al., 1962) and South Africa (Steinke, 1995) while Kairo et al. (2002) also reported an average biomass of 497 t/ha for *Rhizophora* mangroves in northern Kenya.

The partitioning of photosynthate for growth amongst different tree parts varies with species and with time. Factors like age, environmental conditions, forest structure and competitive interactions all have an influence on the proportion of the photosynthate allocated for the growth of roots, stems, branches and leaves (Koslowski et al., 1991). While little is known either quantitatively or qualitatively about such effects in mangroves, analysis of allometric data for trees of different sizes at the same (or similar) site(s) give some insights into the effect of tree size on the allocation of carbon for growth (Clough, 1992). Long term data on mangrove primary production are rare due to difficulties in quantifying canopy production (Alongi, 2002). Reliable estimates have come from a 7-year continuous study in Mexico (Day et al., 1996) where environmental factors such as sediment salinity, air temperature and rainfall were responsible for the inter-annual variability in aboveground biomass production. In East Africa, Kairo et al. (2008) have reported biomass accumulation rate of 24.9 t/ha in a 12 year replanted *R. mucronata* stand in Kenya.

Little work has been done on the potential of mangrove forests to sequester atmospheric carbon. Ong (1993) estimated the rate of carbon sequestered in mangrove mud to be around 1.5 t C ha^{-1} yr^{-1}. Clough et al. (1999) studying biomass production in different aged *R. apiculata* observed a general trend of increase in production up to 25-30 years with older trees having higher carbon fixation rates. Given the global mangrove cover of 170,000 km^2 the total amount of carbon sequestered by mangroves is approximately 25.5 $x10^6$ t C ha^{-1} yr^{-1}. Cebrian (2002) estimates that with the current loss of 35 % of global mangrove cover, this has resulted in a net loss of 3.8×10^{14} g C stored as mangrove biomass. However, this figure does not include belowground biomass estimates. The initial controlled experiments looking at how tree species composition may affect this potential ecosystem function have been initiated in a number of terrestrial sites (Table 1.1). However no controlled studies have looked at this ecosystem function in mangroves and the current work is the first study attempting to investigate this important ecosystem function.

1.4.2 Belowground biomass

Mangrove root systems are concentrated mainly in shallow horizons (top 50 cm) of the soil (Komiyama et al., 1989). They are composed of aerating, absorbing, or anchoring and cable components (Tomlinson, 1986). The aerating component projects aboveground and controls gas exchange to the belowground root system, e.g. columns of prop roots in *Rhizophora* and erect pneumatophores in *Avicennia*. The roots belowground include mainly soft, non-woody (that have little or non secondary thickening) roots less than 10 mm in diameter that produce laterals up to three orders including fine roots, fibrous roots of less than 1 mm in diameter (Gill and Tomlinson, 1977; Clough,1992). The distal part of the growing root is always branch-free (Gill and Tomlinson, 1977). The anchoring roots grow belowground in a vertical direction (Chapman, 1976) and their main function is to support the plant. The cable component extends horizontally from the tree base and unifies the aerating, absorbing, and anchoring parts. For *R. mucronata* this function is carried out by the arches, which are part of the aboveground component. The absorbing component is composed of fine roots that function in nutrient absorption and grow directly from thick, supporting roots (Wada and Takagi, 1988).

Simulation models of nutrient biogeochemistry suggest that the contribution of root production to soil organic matter is more important than litterfall (Chen and Twilley, 1999). Biomass production and accumulation, particularly belowground, provides an important ecological function. These processes contribute to vertical accretion and the ability of mangrove forests to keep pace with sea-level rise (McKee and Faulkner, 2000; Middleton and McKee, 2001). Studies have concluded that accretion rates in mangrove forests in Florida (Cahoon and Lynch, 1997), and Mexico (Lynch et al., 1989) are in equilibrium with reported sea-level rise rates. Studies of belowground biomass and productivity of mangrove forests are also important in estimating root contribution to net primary productivity, and also help identify possible global or local patterns between forest types and species and their response to environmental factors. The information generated is useful in contributing to better understanding of the carbon global cycle and climate change effects on coastal ecosystems. However, there are few estimates of belowground dynamics, such as biomass accumulation or root turnover in mangrove forests and limited information is available about root growth and physiological responses to flooding and/or nutrients (McKee and Mendelssohn, 1987; McKee, 1996; McKee, 2001).

1.5 Soil CO_2 Efflux

Evaluation of carbon fluxes from the biosphere is of critical importance in the face of increasing atmospheric carbon dioxide levels and the associated climate changes (Kuzyakov, 2006; Vincent et al., 2006). Soil respiration, also referred to as soil CO_2 flux, is one of the main fluxes of global carbon cycle, second in magnitude after photosynthesis and accounts for >60 % of total ecosystem respiration (Raich and Schlesinger, 1992; Goulden, 1996; Schlesinger and Andrews, 2000). Forests are particularly important in the carbon cycle, since they contain, respectively, 80% and 40% of the aboveground and belowground global carbon stocks (Dixon et al., 1994).

Sources of CO_2 efflux from the soil can be categorized as: the soil organic matter, above and belowground dead plant residues and organic substances released by living roots such as exudates and secretions (Kuzyakov, 2006). Two groups of organisms are responsible for CO_2 production in the soil; heterotrophic and autotrophic organisms. Heterotrophs can further be subdivided into two broad groups viz; soil microorganisms (Bacteria, fungi) and soil macrofauna (macroscopic invertebrates and meiofauna). Most of the CO_2 produced by the heterotrophic soil organisms is respired by microorganisms such as bacteria and fungi. Although the direct contribution of soil macrofauna is little (Ke, et al., 2005) they increase microbial respiration by fragmenting and mixing of plant residues (Bonkowski et al., 2000) thus intensifying their rapid turnover and increasing CO_2 efflux from the soil (Wardle et al., 1998). Autotrophic respiration is manly performed by plants through root respiration (Kuzyakov, 2006). Other minor autotrophic contributors to soil CO_2 efflux are algae and chemolithothrops (Kuzyakov, 2006).

CO_2 flux is known to exhibit a high spatial and temporal variability. Spatial heterogeneity of CO_2 flux is influenced by a variety of factors including root biomass, microbial biomass, litter amount, soil characteristics or site topography (Epron et al., 2004). Seasonal variations of soil respiration are often associated with either changes in soil temperature (Longdoz et al., 2000) or changes in both soil temperature and soil water content (Davidson et al., 1998). Few studies have been conducted on inter-annual variability in soil CO_2 flux. Inter-annual variations may result from direct effects of environmental actors such as sediment temperature or sediment moisture which could exhibit temporal variation (Epron et al., 2004). For instance, drought has been shown to significantly influence soil CO_2 fluxes (Epron et al., 1999; Savage et al., 2001). Changes in ecosystem processes due to long term ecological variations e.g. forest ageing or disturbances also account for variations in sediment CO_2 flux (Coleman et al., 2002; Alongi, 2002; Epron et al., 2004).

Estimates of soil CO_2 efflux have been made in a variety of ecosystems; however these have mostly focused on terrestrial ecosystems. Few studies have been conducted in marine ecosystem (e.g. Chmura et al., 2003; Lovelock, 2006). Mangroves are relatively less studied ecosystems especially with regard to the emission of greenhouse gases. Being coastal wetlands they are often considered as insignificant sources of CO_2 to the atmosphere (Mukhopadhyay et al., 2002).

1.6 Objectives of the Study

The main aim of the current study was to test how the diversity of mangrove species in replanted mangrove stands affects a range of ecosystem functions, using a fully randomised experiment involving planting three mangrove species in a degraded site. Specific objectives were:

1. To test the effects of mangrove tree species identity, richness, size at planting, sediment depth at planting position and position in the plot, along with a range of environmental factors, on sapling survival.

2. To test the effects of species richness and identity, along with environmental factors, on aboveground productivity and recruitment of wild trees to planted plots.

3. Test the productivity and vertical distribution of roots of different species and species mixes, and to compare these with root biomass from an adjacent naturally growing mangrove stand.

4. To compare temporal variations in the rates of CO_2 flux in replanted mangrove plots and to identify the effects of species mixes and environmental variables on flux rates.

References

Reference at the back

CHAPTER 2: INFLUENCE OF SPECIES RICHNESS AND ENVIRONMENTAL CONTEXT ON EARLY SURVIVAL OF REPLANTED MANGROVES AT GAZI BAY, KENYA

Based on: Kirui, B., Huxham, M., Kairo, J.G. and Skov, M. (2008). Influence of seedling size, positioning and diversity on survival of replanted mangroves at Gazi bay Kenya. Hydrobiologia: 603:171-181

CHAPTER 2: INFLUENCE OF SPECIES RICHNESS AND ENVIRONMENTAL CONTEXT ON EARLY SURVIVAL OF REPLANTED MANGROVES AT GAZI BAY, KENYA

Abstract

Mangrove reforestation projects often suffer from low sapling survival, especially after transplanting saplings from nurseries to reforestation areas. This may be due to the sediment conditions at the target site, the planting strategy or failure to re-establish ecosystem processes. We examined experimentally the influence of environment context, species richness and identity, sapling height and position on sapling survival and environmental variables linked to ecosystem functioning at deforested sites in Gazi Bay, Kenya. At site 1, a high shore location, 32 plots (36 m^2) were planted with 8 treatments: all possible combinations of *Avicennia marina, Bruguiera gymnorrhiza,* and *Ceriops tagal* and an unplanted control (total: 3390 saplings; 4 plots/treatment). At site 2, a low shore location, the influence of sapling height, sapling position and sediment depth were tested by planting with 697 *Sonneratia alba* in a single monospecific plot (341 m^2). After ~2 years, there were significant differences in survival among the three species at site 1 with *Bruguiera gymnorrhiza* recording the lowest survival rate (29 %). Survival was correlated with salinity (a strong effect) and height above chart datum (a weaker effect) at site 1. Sapling position did not significantly affect survival at either site. There was thus no evidence that early survival of transplanted saplings is influenced by the species mix in which they are grown, or by their position in the plot. Rather the tolerance of individual species to salinity was the key to their survival at the high tidal site. Species richness also had no significant effects on environmental variables in the plots. The former presence of a species at a site does not guarantee it will succeed there again if environmental degradation has exceeded species' tolerance.

Keywords: Environmental context, Kenya, Mangrove reforestation, Salinity, Species richness and ecosystem function, Survival.

2.1 Introduction

Mangrove ecosystems provide a wide range of ecological, environmental and socio-economical services (Ewel et al., 1998). Despite these benefits, mangroves are threatened with destruction all over the world through various forms of development and human pressure (FAO, 2003). Over-exploitation to meet rising wood requirements is the main threat to Kenya's 54,000 ha. of mangroves (Dahdouh-Guebas et al., 2000; Abuodha and Kairo, 2001). While various strategies have been employed to encourage sustainable management of mangroves globally, little information is available from East Africa. As is the case in most areas of the world, mangrove reforestation has proceeded without prior site assessment often giving mixed results, for instance Kairo et al. (2001) observed that survival rates of saplings varied between 10 % in areas heavily exposed to wave action to 70 % in well-protected areas nine months after transplanting.

Sapling establishment and early growth are critical phases in the life of a plant. Factors known to influence mangrove sapling establishment include: tidal regime (Rabinowitz, 1978), soil characteristics (McKee, 1995; Minchinton, 2001), seed provenance (Kairo et al., 2001), dispersal (Minchinton, 2006) and predation of propagules (Robertson et al., 1990; Minchinton and Dalby-Ball, 2001; Sousa et al., 2003). Several other factors have the potential to influence survival, particularly in artificial regeneration using saplings, but have received little attention. These include the use of single or mixed species stands, sapling size, position of a sapling in the plot, the proximity and species identity of planted neighbouring saplings and the depth of the substratum.

The most efficient method of mangrove restoration is often to allow natural regeneration (Cintron-Molero, 1992). However, the removal of mangroves can result in physical and biological changes to a site, such as increased sediment salinity, high insolation, loss of nutrients, and disruption of critical species interaction (Zedler et al., 2001; Lewis, 2005). Such changes may make natural establishment of seedlings impossible, leaving sites with no natural regeneration decades after disturbance. However, reforestation of such degraded sites may still be possible especially if it involves the use of transplanted saplings, which are grown in nurseries during the critical, and most sensitive, first few months of life, rather than planting propagules directly into restoration areas which generate poor survival in tough conditions (Kairo, 1995; Toledo et al., 2001). The present study involves such transplantation of nurseried saplings with heights ranging from 15 to 45 cm. Sapling size at transplanting may have a major effect on survival, for example; larger saplings can withstand wave action and siltation better than small saplings; however, large saplings might also be more vulnerable during transplantation, because the rhizosphere is more extensive and therefore prone to breaking during handling. The position of plants within reforestation plots may also influence growth and survival of the sapling. Saplings at the edge of plots may show better survival due to less competition for resources (e.g. light and nutrients) compared to the saplings in the middle of the plot. Alternatively, trees close to the edge may suffer 'edge effects', such as wind throw or drag and erosion due to water currents (e.g. Saunders et al., 1990; Laurance and Yensen, 1991; Gascon et al., 2000).

Most mangrove reforestation projects have involved planting a single species, with the objective of wood production or to control soil erosion (Lewis, 2005). The reasons for single-species planting are typically that certain species have higher cash-crop value, and/or are easier to plant (Kelty, 2006). However, mono-specific planting ignores the possibility that species mixing might be an inherent requirement for full ecosystem function and that a reduction in species richness may depress ecosystems' capacity to deliver their goods and services, such as biomass production. Thus, elevated species richness has been shown to boost ecosystem productivity in grassland, wetland and microbial systems (Naeem et al., 1994; Tilman et al., 2002). However, due to difficulties in manipulating long-lived species like trees, few attempts have so far been made to experimentally test the effects of species richness in forest systems (Table 1.1, Parrotta, 1999). It is possible that species richness could influence tree survival positively by allowing mutualistic or complementary interactions or negatively through, for example, interspecific competition (Kelty, 2006). The relationship between tree species richness and ecosystem functional responses has never been experimentally addressed in mangroves.

The present study contained two experiments (at sites 1 and 2) with the following objectives:

1) To test the effects of species mixture, species identity and the

environmental context on sapling survival.

2) To test the effects of sapling position on survival.

3) To test the effects of sapling height and sediment depth on survival.

4) To test the effects of species mixture on environmental variables linked to ecosystem functioning.

Objectives 1, 2 and 4 were tested at site 1; objectives 2 and 3 were tested at site 2.

2.2 Materials and Methods

2.2.1 Study area

The study was conducted at Gazi bay (4°25'S and 39°50'E) situated on the south coast of Kenya, about 50 km from Mombasa (Figure 2.1). The bay is sheltered from strong waves by the Chale Peninsula to the east and a fringing coral reef to the south. Two seasonal rivers drain into the bay and groundwater seepage is restricted to a few points (Tack and Polk, 1999). Total annual precipitation (1000-1600mm) falls mainly in two rainy seasons (April-August and October-November). Air temperature is 24-39°C and relative humidity averages

95%. All the nine species occurring in Kenya are found in Gazi bay. The spring tidal range in Gazi bay is ~4.0 m (Kitheka, 1997).

The mangrove forests of Gazi bay have been exploited for many years especially for building poles and fuel-wood (Kairo, 1995; Bosire et al., 2003). Clear-felling due to the industrial extraction of fuel wood left large contiguous blank areas. Two sites were used in the present experiment. Site 1, covering >3000 m^2 (Figure 2.1), is located in an area that has remained barren for over 20 years after clear-felling a previous stand comprising of *Xylocarpus granatum* König 1784 (not included among the replanted species due to logistical difficulties in obtaining enough seeds) and *Bruguiera gymnorrhiza* (L.) Lamk. 1797-8 (Bosire et al., 2003). The site borders the landward side in the inundation class IV of Watson (1928) i.e. flooded only at spring high tides. The topsoil at the site is sandy while the subsoil is peaty sand. Site 1 is divided into two similar sized areas (block 1 and 2 ~1500 m^2 each). Site 2 is a stretch of beach that receives daily tidal inundation (Watson inundation class 1) and has moderate wave exposure and sandy sediments. The site was previously covered by a fringing *Sonneratia* forests with a width of ~ 40-70 m deep and ~800 m long. In the 1980s' close to 300m of this forest was cleared for fuel wood (Kairo, 1995). As a consequence, site 2 experiences coastal erosion resulting in coconut palms in the adjacent agricultural field being washed into the sea.

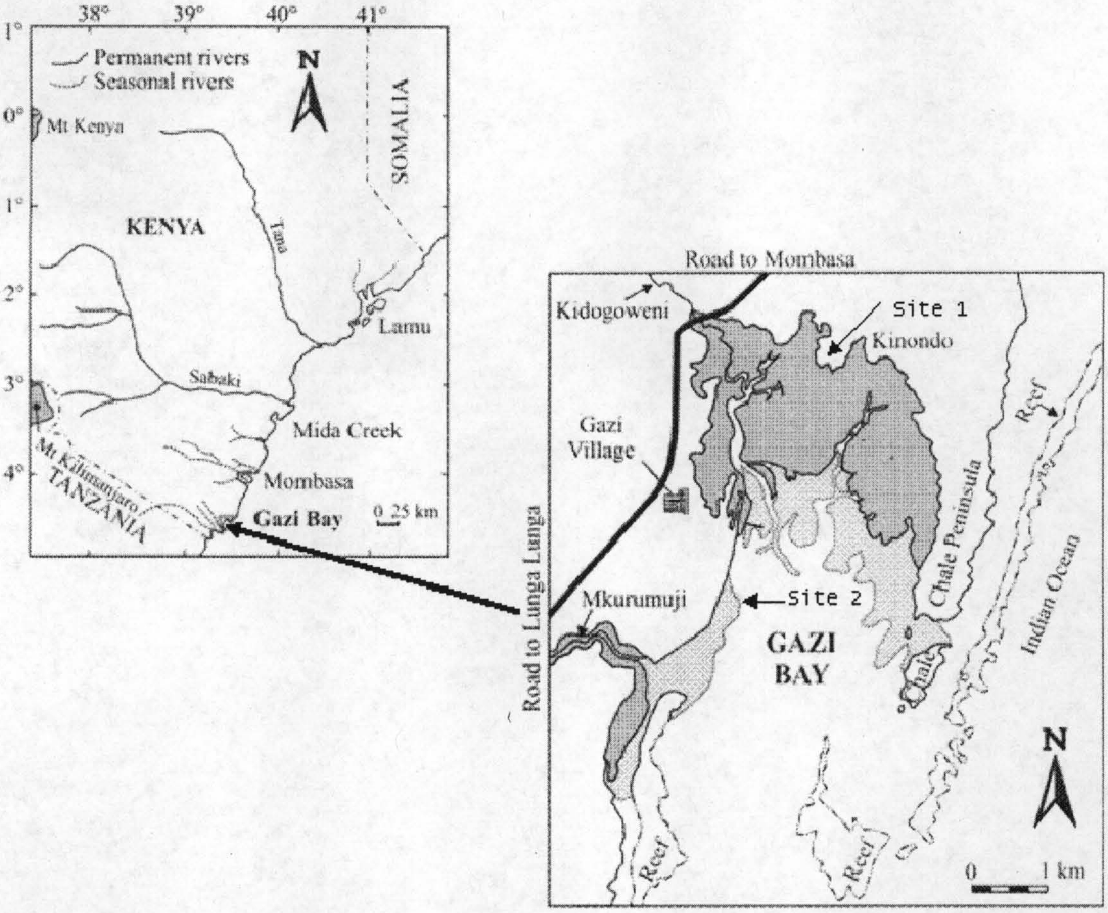

Figure 2.1: Map of the study area: dark grey shade = mangrove cover; light grey = seagrass formation (modified from Bosire et al., 2003)

2.2.2 Experimental Design

2.2.2.1 Species richness experiment (Site 1)

Thirty-two 6 m by 6 m plots were established at site 1, separated into two blocks with 16 plots in each. Planting distance between saplings was 0.6 m giving a total of 121 saplings per plot. Each plot was separated from each other by a border of at least 10 m. Plots were planted with mixes of *Avicennia marina* (Forssk.) Vierh, *B. gymnorrhiza* and *Ceriops tagal* (Perr.) C.B. Robinson 1908. Six mangrove species occur on the landward side of Gazi bay; however, *Avicennia* ('A'), *Bruguiera* ('B') and *Ceriops* ('C') were selected as they were the dominant species in the adjacent natural stand. There were three species-richness levels: 1 tree species, 2 tree species and 3 tree species, plus an unplanted control ('Con', 0 species). To enable the separation of the effects of species richness from species identity in the analysis i.e. effects due to the chance inclusion of a species with disproportionately strong influence on the response (Scherer-Lorenzen et al., 2005) each species richness level was represented by all possible combinations of the three species, i.e.: three 1-species treatments (A, B or C), three 2-species treatments (AB, AC, BC), and one 3-species treatment (ABC). The eight treatments were randomly allocated to plots, giving 2 replicate plots per treatment per block. Plots were planted in August 2004 using 6-month old nursery saplings, ranging in size from ~20 to ~45 cm height depending on species; saplings were randomly allocated to appropriate treatments. All transplanting was carried out in the early morning at low spring tide. The pots were carefully removed during planting to avoid tampering with the root system and saplings were placed in holes dug using spades. All dead saplings were replaced after one month and subsequently no more replacements were made; hence subsequent survival data did not include mortality due to immediate transplantation shock.

The following environmental variables were measured before planting at site 1: a) redox potential, b) pore water salinity, c) sediment organic carbon content, d) sediment grain size, e) sediment temperature and f) plot height above chart datum. Areas <1 m from plot edges were not sampled to avoid 'edge effects', and for each variable (except f) results for each plot were means for four random sub-samples. Sediment at 10 cm depth was obtained for redox and salinity measurements using a D-section soil corer. A portable redox meter was used to record redox measurements; pore water salinity was measured by taking approximately 50 g sediment for centrifuging in the laboratory and salinity measured from the extracted pore water using a hand-held refractometer. Surface scrapes (to 1 cm depth) were taken for grain size and carbon analysis; the percentage of silt and coarse sand in surface scrapes were calculated following manual sieving, and the percentage carbon was calculated as loss on ignition at 480°C (Eleftheriou and McIntyre, 2005). Surface temperature was measured at midday on a clear sunny day (probe inserted to 1 cm below sediment surface). The heights of each of the plots above chart datum were recorded using a theodolite. Sapling survival was assessed monthly for 416 days, with the position and identity of dead trees recorded. All other environmental variables (excepting f) were subsequently measured every 6 months.

2.2.2.2 Single species experiment (Site 2)

A total of 697 nursery raised *Sonneratia* saplings were planted at site 2 in July 2003 during spring low tide (plot height above datum at this site was 1.7m). Planting was carried out in a matrix inside a 22 x 16 m plot. Most saplings were 4-5 months old, but these were supplemented with plants ranging up to ~12 months. Saplings ranged from 5-105 cm high (as measured from the substrate surface to the apical bud), and were planted randomly within the plot. This relative variability allowed us to test effects of initial sapling height on survival. Planting was done at low spring tide, with 1 m x 0.5 m spacing between plants (giving a total of 697 plants; the final row had a spacing of 1m rather than 0.5m between saplings). One month after planting, the site was revisited and any dead and washed away plants were replaced. Survival was subsequently monitored every two months for a period of 25 months, with the position of any dead sapling noted. Substrate depth (to a maximum of 50 cm depth) was measured before planting at each planting hole; a coral bedrock emerges at places at this site, and we speculated that trees in shallow sediment might suffer higher mortality. Sapling height and stem diameter (at 10 cm above sediment) were measured at planting time and periodically afterwards.

2.2.3 Statistical analyses

The effect of species richness at site 1 on the mortality of each species was explored using 2-factor (treatment, block) general linear model ANOVAs (GLM). Separate GLMs were run for each species after checking for heterogeneity of variances and log transforming where necessary. The final percentage mortality of each species in each treatment was the response variable; hence this was a percentage of a total of 121 trees for monospecific plots, 60 for two species and 40 for three species plots. Treatment (monospecific, with either one of the other two species or with both the other species, giving 4 treatments for each species) was a fixed factor and block a random factor. The effects of planting treatment on the measured environmental variables were also explored using GLMs with the same factors and the final values of each environmental variable (taken after 416 days) as response variables. The relationships between survival, sapling species and initial environmental variables (used this time as predictor variables) measured for each plot at site 1 were examined using Cox regression. This is a semi-parametric multiple regression technique designed to deal with non-normal survival data with a clearly defined time origin, clearly defined definition of 'failure' (in the present case, death) and a mixture of individuals that 'fail' and those that are 'censored' (i.e. that survive until the end of the study, or are withdrawn for some reason (Collett, 1994)). A similar Cox regression was performed for site 2 data to explore the effects of initial sapling height and sediment depth on survival. The effects of planting position within a plot on survival were tested at both sites using chi-squared analyses, which compared the spatial distribution (trees at the plot edge were compared with the trees at different distance from plot edge) of observed survival for each tree species against the null distribution assuming no spatial effects; hence for site 1 three distributions were produced, one for each species summed across all plots containing that species, whilst for site 2 a single distribution was produced. Statistical analyses were performed using Minitab 14 and SAS 9 software.

Table 2.1: Means (± s.d.) of survival of each species and of the environmental variables in the different species treatments at site 1. Survival was measured after 416 days, and all the environmental variables show initial values. A= *A. marina*, B=*B. gymnorrhiza*, C=*C. tagal*. n = 4 in each case; survival data for mixed species plots is separated into relevant species

Species treatment	Species	Survival (%)	Salinity	Redox (mv)	Height above datum (m)	Temperature (°c)	Grain size (%)			Organic Carbon (%)
							Silt (<63 µm)	Medium sand (63-500 µm)	Coarse sand (>500 µm)	
A	A	86.2 ± 8.5	64.3 ± 8.5	223.3 ± 21.0	3.3 ± 0.1	28.1 ± 0.1	18.0 ± 1.8	57.2±2.6	24.8 ± 4.0	20.8 ± 2.2
B	B	38.6 ± 23.8	50.0 ± 9.3	200.7 ± 13.0	3.2 ± 0.1	28.4 ± 0.5	19.1 ± 2.9	57.7±4.9	23.2 ± 4.4	17.7 ± 12.2
C	C	87.3 ± 5.3	59.3 ± 8.1	181.0 ± 58.4	3.3 ± 0.9	28.1 ± 0.3	20.7 ± 16.7	51.4±24.6	28.0 ± 8.7	19.9 ± 7.5
A*B	A	90.5 ± 9.3	58.3 ± 13.8	200.4 ± 26.1	3.3 ± 0.1	28. 1± 0.1	12.8 ± 2.7	64.2±8.8	23.0 ± 6.7	21.1 ± 5.0
	B	22.4 ± 24.4								
A*C	A	89.7 ± 9.0	51.7 ± 6.0	199.4 ± 13.6	3.2 ± 0.1	28.4 ± 0.5	17.7 ± 4.7	58.5±8.6	23.8 ± 4.6	24.5 ± 3.6
	C	64.3 ± 24.4								
B*C	B	16.9 ± 8.4	54.0 ± 4.2	213.8 ± 21.3	3.3 ± 0.1	28.1 ± 0.3	14.6 ± 1.4	65.3±6.9	20.1 ± 6.4	26.4 ± 10.6
	C	66.1 ± 14.7								
A*B*C	A	86.5 ± 9.0	68.0 ± 10.3	202.6 ± 19.3	3.2 ± 0.1	28.6 ± 0.5	19.5 ± 3.7	59.6±7.5	20.9 ± 3.8	26.6 ± 12.9
	B	32.5 ± 35.7								
	C	68.8 ± 32.9								
Control	-	-	64.3 ± 16.2	199.2 ± 29.0	3.3 ± 0.1	28.1 ± 0.2	12.0 ± 1.9	67.0±7.2	22.9 ± 4.6	18.3 ± 5.5

*Salinity is a scale hence without units (McLusky and Elliot, 2004)

2.3 Results

2.3.1 Species mixture, identity and the environmental context on sapling survival

Of the environmental variables, granulometry and salinity showed the largest relative initial variability between plots (although randomization meant there were no significant differences between treatments; Table 2.1). 416 days after planting there were large differences in the mean survival of the three species: 87, 29 and 71 % survival for *Avicennia, Bruguiera* and *Ceriops* respectively. Survival was not influenced by the identity of the species richness for any of the three species (D.F. = 6, $p > 0.05$) hence individual trees were treated as independent for the purposes of Cox regression. The best Cox regression model (selected to include significant variables and on the basis of the goodness of fit value) took the form: time to death = species, plot height, salinity, species × salinity, with a total of 66 % of data censored (that is, 66 % of all trees had survived). The global test was highly significant (likelihood ratio test, d.f. = 4, $p < 0.0001$), as were the effects of salinity and species identity (Figure 2.2).

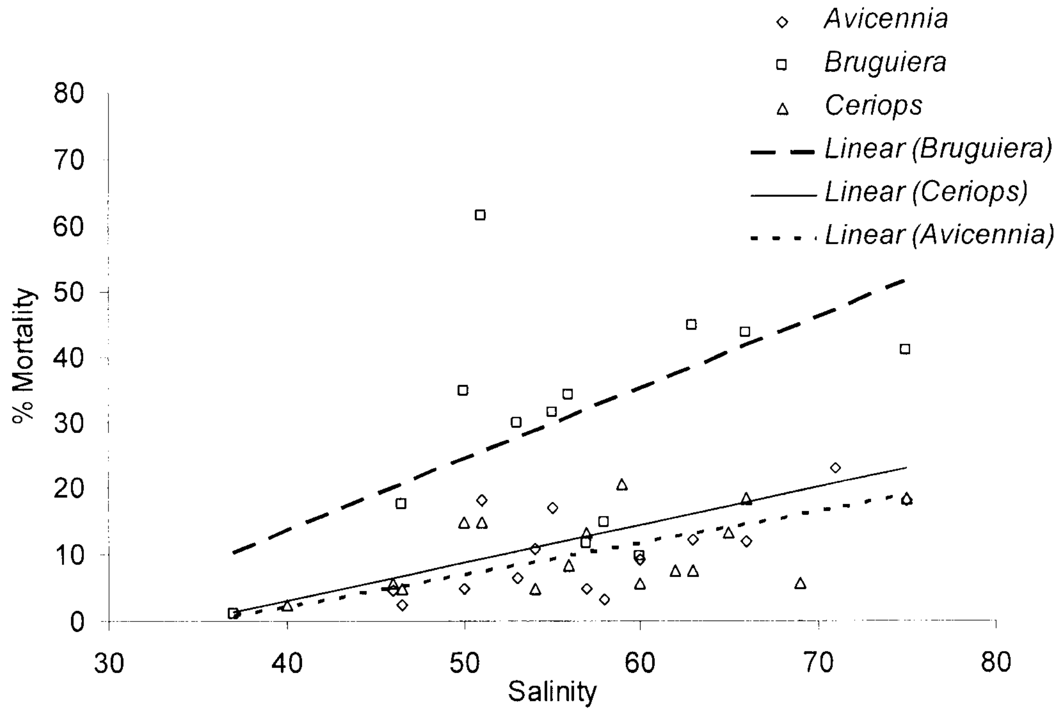

Figure 2.2: Relationship between initial plot salinity and mean sapling mortality at Site 1. Separate linear regression lines are shown for each species for illustrative purposes only; a more robust statistical analysis is given in Table 2.2.

In this regression, the comparator species was *Avicennia*. Hence *Bruguiera* showed a highly significant increased risk of mortality, compared with *Avicennia*, of 5.89 over the period of this study (this risk is given as the hazard ratio; Table 2.2). The effect of salinity was also highly significant, with each increase in salinity unit increasing risk of mortality by 1.04. These analyses were based on the initial salinity measurements; during the course of our sampling salinity showed seasonal variation, ranging from a mean across plots of 54.98 to 80.79. The responses of each species to salinity were different (Figure 2.2) giving a significant overall species × salinity interaction term (Table 2.2). Differentiating these interactions between species showed the response of *Bruguiera* to salinity was highly significantly different (D.F. = 1, P = 0.008) compared with *Avicennia*, whilst *Ceriops* showed a significantly different response (D.F. = 1, p = 0.044). Surprisingly, height above chart datum showed a significant negative relationship with mortality risk (Table 2.2).

Table 2.2: Results of Cox regression of time to death for trees at site 1, showing hazard ratios for the significant variables. *Avicennia* was the comparator species. Hazard ratio equates to the level of increased risk of mortality compared to that of *Avicennia*; the higher the Hazard ratio, the higher the risk

Variable Name	d.f.	p	Hazard Ratio
Bruguiera	1	<0.0001	5.89
Ceriops	1	<0.0001	2.10
Salinity	1	<0.0001	1.04
Height above chart datum	1	0.02	0.99
Species × Salinity	2	0.025	-

2.3.2 Sapling position on survival

The position of a sapling in the plot, measured as distance from the edge, had no effect on survival for any species at site 1 (chi-squared test, D.F. = 1, p>0.05;

Figure 2.3). Overall, 62 % of the trees at the edge of the plots survived compared to 67 % of the interior saplings.

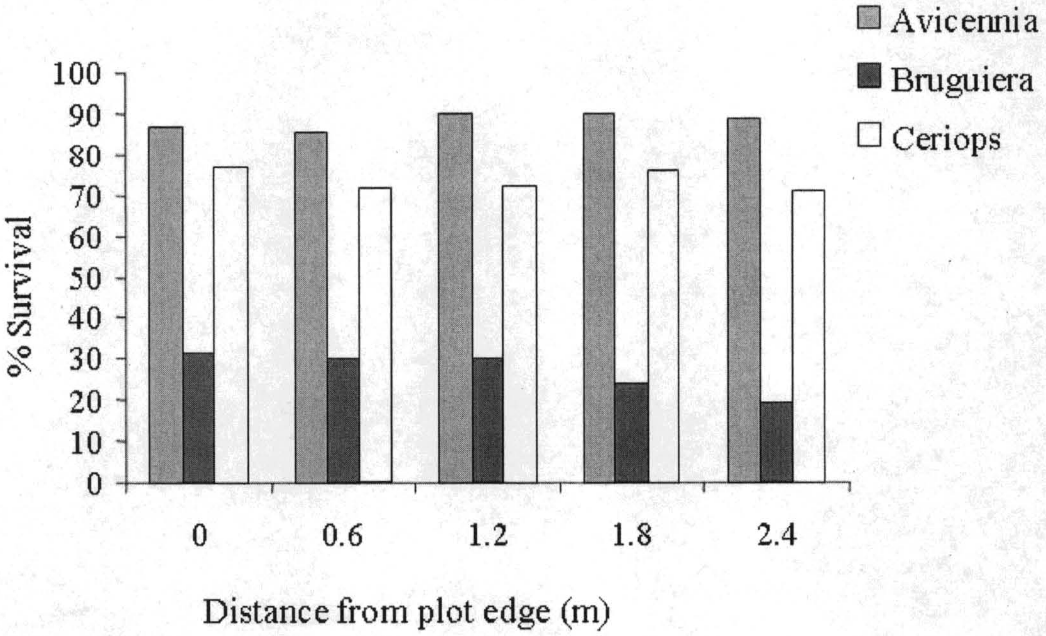

Figure 2.3: Sapling survival from the edge towards the interior of plots at site 1

Similarly, distance from the edge of the plot had no effect on sapling survival at site 2 (chi-squared test, D.F. = 1, p>0.05; Figure 2.4). Fifty two percent of the edge trees survived compared to 47 % of the interior trees.

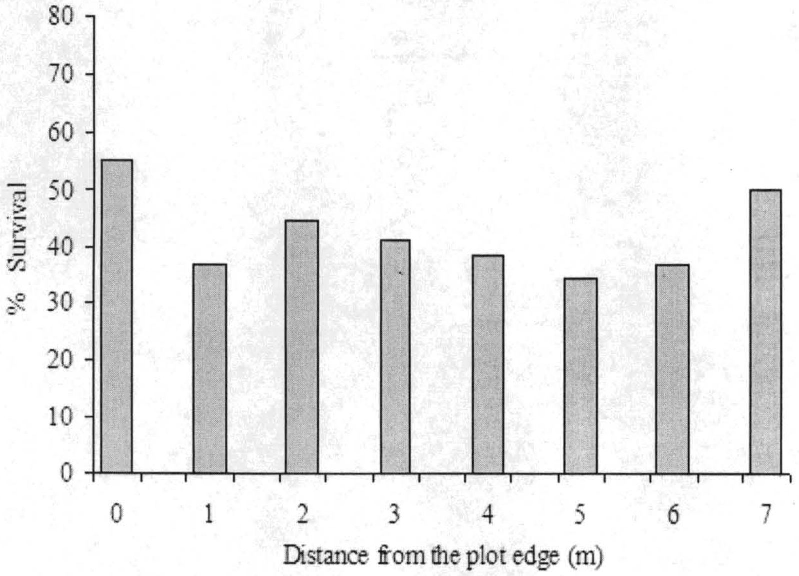

Figure 2.4: Sapling survival from the edge towards the interior of plots at site 2.

2.3.3 Sapling size at planting

There was no effect of sapling height at the time of planting on survival at site 2 (Cox regression, D.F. = 1, $p > 0.05$) however, the relationship approached significance with a weak negative relationship ($p = 0.06$) between the height of a sapling at planting and survival. Most *S. alba* saplings heights at planting ranged between 10 and 20 cm (Table 2.3.)

Table 2.3: Height class of *Sonneratia alba* at site 2

Height size-class (cm)	No of saplings
1-10	294
10-20	299
20-30	46
30-40	25
40-50	22
50-60	9
>60	10

2.3.4 Substrate depth

We found no significant effect on survival of the depth of sediment to the bedrock at each planting hole at site 2 (Cox regression, D.F. = 1, $p>0.05$).

2.3.5 Species mixture on environmental variables linked to ecosystem functioning

We found no significant effects of sapling species treatments on a range of environmental variables of relevance to ecosystem functions measured at site 1 (Table 2.4). Most variables did show significant differences between the two blocks at this site, but this reflects initial conditions. Plants of all species in block 2 showed higher mortality than in block 1 with block 2 having substrate with lower mean silt and carbon contents and higher mean salinities.

Table 2.4: Two-way ANOVA of the environmental variables at site 1. In all cases analyses were performed on variables measured after 416 days (i.e. as potential response variables).

Variable	Factor	D.F.	MS	P
Salinity	Block	1	33.0	0.07
	Treatment	7	61.0	0.08
	Interaction	7	21.0	0.87
	Error	15	48.0	
Redox	Block	1	82.2	0.07
	Treatment	7	22.7	0.40
	Interaction	7	18.7	0.07
	Error	15	7.5	
Temperature	Block	1	0.3	0.65
	Treatment	7	1.9	0.25
	Interaction	7	1.01	0.83
	Error	15	34.1	
Sand	Block	1	300.9	0.04
	Treatment	7	49.1	0.49
	Interaction	7	48.2	0.17
	Error	15	408.9	
Silt	Block	1	361.9	0.01
	Treatment	7	40.9	0.36
	Interaction	7	30.6	0.37
	Error	15	387.7	
Organic carbon	Block	1	36.9	0.00
	Treatment	7	2.7	0.31
	Interaction	7	1.8	0.49
	Error	15	1.9	

2.4 Discussion and Conclusion

We found no species richness effects on sapling mortality or indeed on a suite of other environmental variables - sediment % silt, carbon, salinity, redox or surface temperature. We anticipate that effects may become apparent as trees mature. For example, the closure of the canopy should cause differences between unplanted controls and planted plots in sediment characteristics, and given the better survival of *Avicennia* these effects should manifest faster in plots with this species. In a laboratory experiment, Cardona-Olarte et al. (2006) found that increased salinity stress reduced the strength of inter-specific competition, increasing the likelihood of facilitative interactions between species at higher levels of stress; such facilitative plant interactions have been observed in other shoreline systems (Bertness and Hacker, 1994). However, our data show that any such putative beneficial effects of species mixing do not manifest early enough to help with initial sapling establishment.

Salinity was shown to have a clear effect on sapling mortality, in particular on *Bruguiera*. Mangrove trees generally achieve optimum growth at low to moderate salinity levels (Ball, 2002). However different species show different distributions in the field with respect to salinity, which may reflect variations in requirements and tolerances for salts (Ball, 1988; Table 2.5). *Bruguiera* usually occupies the middle intertidal zone where optimal growth occurs at soil salinity levels of 8-26, and higher salinities tend to reduce its biomass and also result in high mortality for both saplings and trees (Naidoo, 1990). However, *Bruguiera* distribution can span well beyond the middle intertidal zone; for example, it used to occur at site 1 before the original forest was removed (Kairo, 1995) and some mature trees can be observed at extreme high water in Gazi bay. Indeed, we planted this species here because of its former occurrence at the site, and since it has healthy growth in adjacent natural stands. In contrast, *Avicennia* and *Ceriops* have a wide range of salinity tolerances due to their conservative water-use characteristics (Tomlinson, 1986) and *Avicennia* has possibly the widest intertidal range of East African mangrove species.

Table 2.5: Global comparison of studies on substrate salinity range by species in the three study genera: A=*Avicennia*, B=*Bruguiera*, C=*Ceriops*

Species	Substrate salinity range	Study area	Author(s)
A. marina	10-55	Eastern Australia	Saintilan, 1998
A. marina	0-35	Hong Kong	Yong et al., 2005
A. marina	8-200	Australia	Ball, 1988
A. marina	0-100	Japan	Wakushima, 1994a
A. marina	40-89	This study	
A. germinans	43-259	Colombia	Elster, 2000
B. gymnorrhiza	0-80	Japan	Wakushima, 1994a
B. gymnorrhiza	0-35	Thailand	Wakushima, 1994b
B. gymnorrhiza	40-89	This study	
B. sexangula	2-10	Hawaii	Krauss and Allen 2003
C. tagal	8-40	Thailand	Wakushima, 1994b
C. tagal	0-110	Australia	McGuiness, 1997
C. tagal	0-80	Australia	Clarke et al., 2001
C. tagal	40-89	This study	

Our experimental observations are thus broadly consistent with studies on mangrove distribution in the field. For example, Lopez-Hoffman et al. (2006) reported that Rhizophoreceae species could establish in high salinity areas, but failed to grow into maturity, whereas *Avicennia* species did achieve maturity in these areas. A study of mangrove distribution in Venezuela (Medina and Franscisco, 1997) reported higher prevalence of *A. germinans* in open sites experiencing high salinities and drought compared with *Rhizophora mangle.* Many other studies support the importance of salinity as a factor controlling survival (Table 2.5). Our results conform to this conclusion, particularly as our study site is a relatively small and homogeneous area and thus the effects of salinity on survival are not confounded by large differences in potentially important variables such as tidal height, crab predation and shading. A significant hazard ratio of less than 1 for height above chart datum was a surprising result for site 1, implying increasing height above sea level decreases mortality. This probably shows simply that small differences in height above chart datum can be misleading as surrogates for inundation period; although block 1 was marginally higher than block 2 at site 1, most of the environmental variables (and personal observations) showed that it was inundated by the tide for slightly longer.

Clear-felling of trees and subsequent exposure of bare land for long periods has been shown to lead to shifts in soil physico-chemical characteristics as well as gross changes in biological communities impairing natural regeneration (Zedler et al., 2001; Lewis, 2005). Such changes necessitate human intervention for ecosystem restoration (Bosire, 2006). The high tidal elevation of the plots at site 1 combined with high rates of evaporation due to long periods of exposure could be responsible for the salinity levels observed, which are likely to be higher than those found under the previously intact canopy (Krauss and Allen, 2003; Lopez-Hoffman et al., 2006).

There was evidence that sapling size in *Sonneratia* had a negative effect on survival: size effects approached significance in the regression. Hence for locations with similar environmental conditions as site 2, our study provides no support for the idea of keeping saplings in a nursery to grow for longer periods than three months before transplantation, which means that the costs per tree can be reduced. Because position in the plot made no difference to survival of saplings at either of our sites, we conclude that edge effects were unimportant. Hence the size and shape of plots established during restoration work at similar sites are unlikely to be important in factors influencing success.

Previous studies have observed that saplings grown under shade conditions suffer particularly badly from the stress of transfer to harsh environmental conditions with full light exposure (Toledo et al., 2001; Krauss and Allen, 2003). Smith (1987) found significant differences in the survival of saplings of four species across different light levels: survival under full exposure was greatest for *Rhizophora* followed by *Ceriops*, *Avicennia* and finally *Bruguiera* suggesting that exposure to full sunlight was the main factor limiting *Bruguiera* survival. To redress the problem of salt-stress susceptibility by the saplings, Toledo et al. (2001) suggests the need to develop an outdoor nursery system independent of tides. We cultured our saplings in nurseries and habituated them to the harsh environmental conditions by gradually exposing them to increasing levels of sunlight, nevertheless at both our experimental sites there were high mortality rates during the first few months following transplantation. This mortality is not easily negated as it may be due to a range of interacting stresses, including those we attempted to limit.

In conclusion, mangrove trees are usually planted at a young age (<1 year) and as such may be highly susceptible to a range of environmental stresses. Salinity was the major stress controlling survival at site 1. There was no evidence that the survival of a species was influenced by the species mix in which it was planted. Hence the success of restoration programs in clear-felled lands left exposed for long periods largely hinges on planting species with tolerance traits to adverse factors specific to the location. Because sites may undergo hydrologic and other physical changes after being cleared, the former presence of a species at a site does not guarantee that it will succeed there again.

Acknowledgement

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References

References at the back

CHAPTER 3: EFFECTS OF SPECIES RICHNESS, IDENTITY AND ENVIRONMENTAL VARIABLES ON GROWTH AND RECRUITMENT IN PLANTED MANGROVES

Based on: Kirui, B., Huxham, M., Kairo, J.G. Skov, M. and Mencuccini, M. Effects of species richness, identity and environmental variables on growth and recruitment in planted mangroves. (Manuscript)

CHAPTER 3: EFFECTS OF SPECIES RICHNESS, IDENTITY AND ENVIRONMENTAL VARIABLES ON GROWTH AND RECRUITMENT IN PLANTED MANGROVES

Abstract

Anthropogenic impacts on biodiversity across a wide range of ecosystems are now well documented; however the responses of ecosystems to reduced diversity are still poorly understood. We investigated the effects of species richness, species identity and environmental variables on aboveground biomass increment and on naturally recruited saplings using replanted experimental mangroves at Gazi bay, Kenya. 32 plots (36 m^2) were planted with 8 treatments: all possible combinations of the trees *Avicennia marina*, *Bruguiera gymnorrhiza,* and *Ceriops tagal* and an unplanted control (total: 3390 saplings; 4 plots/treatment). Trees were planted in July and August 2004 and monitored annually until 2007.

Growth was slow in the first two years of the study, but by 2007 there was a significant treatment effect on aboveground biomass. *Avicennia marina* showed strong competitive traits; with the best growth overall and enhanced growth of individual trees when planted in mixed species plots. The highest biomass was recorded in three species mixes; partitioning the net effects of species mixing showed a strong species selection effect, but there was also a complementarity effect in some of the three species plots. Biomass was positively correlated with initial plot height above sea datum level and negatively correlated with sediment salinity, ammonium and phosphate concentration. A facilitation effect was observed in the recruitment of wild saplings, with *Avicennia* acting as a 'nursery species' for recruits of other species, particularly *Ceriops tagal.*

Key words: Aboveground biomass, biodiversity and ecosystem function, facilitation, Kenya, Mangrove reforestation.

3.1 Introduction

The growing awareness of human domination of Earth's ecosystems, and the resulting reduction in species diversity in many habitats worldwide (Vitousek et al., 1997; Kareiva et al., 2007), has stimulated interest among ecologists in understanding the relationship between biodiversity and ecosystem function (see reviews in Schwartz et al., 2000; Loreau et al., 2002; Hector, 2002; Schmid et al., 2002; Hooper et al., 2005; Spehn et al., 2005; Diaz et al., 2006). Numerous attempts have been made to investigate this relationship experimentally and by using comparative approaches; to date, the most compelling evidence for strong linkages has come from experiments in grassland ecosystems in which species diversity was manipulated directly in replicated treatments (Tilman et al., 1997; Hector et al., 1999).

There was criticism of some of the earlier work for failing to account for the influence of 'selection effect' i.e. where diversity effects are caused by the greater chance of inclusion of one or few dominant, high biomass species being in the mix and the 'niche complementarity effect' which states that differences in niches between species should lead to efficient resource utilization and consequent high productivity (Loreau and Hector, 2001; Fargione et al., 2007). In addition, studies that use only a small fraction of the relevant species pool at a given site may not produce results that are applicable under natural conditions. Although grasslands still predominate in the literature, there are now increasing numbers of studies from other ecosystems, including freshwater

(McGrady-Steed et al., 1997; Naeem and Li, 1997) and marine (e.g. Emmerson and Huxham, 2002; Bruno et al., 2005). However, the ecological significance of diversity remains unknown in many systems. For example, it is uncertain what relevance studies on short-lived non-woody plants have to woody ecosystems such as forests. Long-term manipulative experiments using trees have recently been initiated at a number of sites across Europe (Scherer-Lorenzen et al., 2005 Scherer-Lorenzen et al., 2007), but are unlikely to yield results rapidly. No manipulative experiments using tropical species have been conducted.

Mangroves are trees found in estuaries and intertidal zones in tropical and subtropical regions (Tomlinson, 1986). Whilst the mangrove ecosystem supports a relatively low diversity of plant forms it is rich in other organisms, for instance arthropods, molluscs, fish and birds (Field et al., 1998). A relationship between species diversity and ecosystem functions has been inferred (MacNae, 1968; Field et al., 1998), but never tested in mangrove ecosystems. Previous survey studies that have used comparative approaches (e.g. Caspersen and Pacala, 2001) have focused on the influence of management systems and tree identity on ecological functions; they have generally emphasized the roles of nutrient and carbon fluxes in determining the net primary productivity of the single dominant mangrove species (e.g. Gong and Ong, 1990; Mukhopadhyay et al., 2006). Whilst comparative methods can provide useful information on the main drivers of ecosystem function, they usually cannot explain the underlying mechanisms behind relationships (Huston, 1997), and can obscure within-habitat variations (Schmid, 2002). Mangroves are naturally species poor, which means the manipulation of most of the species present is feasible, and do grow relatively fast (Kairo, 1995). However, to our knowledge, no within-site experiment has been conducted in a mangrove ecosystem where species diversity was manipulated.

In July 2004, a long-term experiment, measuring a range of ecosystem functions, was established in Kenya. The experiment used three species (*Avicennia marina* (Forssk.) Vierh, *Bruguiera gymnorrhiza* (L.) Lamk. 1797-8 and *Ceriops tagal* (Perr.) C.B. Robinson 1908) that grow sympatrically near the experimental site, and created diversity treatments containing all possible species combinations. This chapter presents early findings on the effects of species diversity and soil conditions on aboveground biomass productivity and on the recruitment of wild seedlings ('wildings'). The null hypotheses were:

1) Species diversity and identity of mangroves has no effect on the aboveground productivity of planted plots.

2) Species diversity and identity of mangroves has no effect on the natural recruitment of mangrove saplings to planted plots.

3) Aboveground productivity is not influenced by variations in environmental factors such as salinity, height above sea level, redox and carbon content of the soil.

3.2 Materials and Methods

3.2.1 Site description

The study was conducted at Gazi bay (4°28'S and 39°29'E) located on the southern coast of Kenya ~55 km from Mombasa city (Figure 3.1). It is a shallow coastal ecosystem with extensive mangrove formations intersected by two creeks. The total area of the bay excluding the area covered by mangroves is 10 km^2. Two seasonal rivers (Kidogoweni and Mkurumudji) drain into the bay and there is restricted groundwater seepage (Tack and Polk, 1999). Seasonal rains dominate the local climate with two rainy seasons: heavy rains in April to June and lighter short rains in October to November. The total annual rainfall ranges between 1000 to 1600 mm. The average annual temperature is 26°C with daily variation between 24°C and 39°C (Bosire et al., 2003).

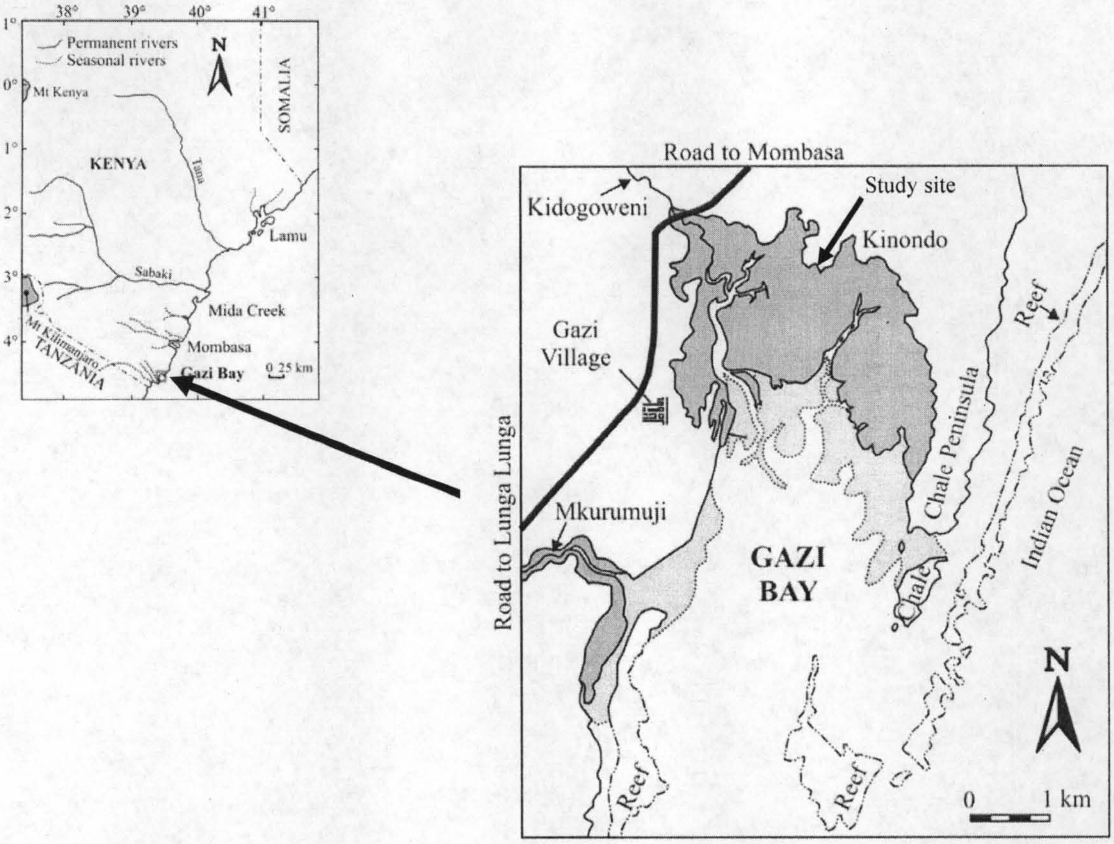

Figure 3.1: The study area: dark grey shading = mangrove cover; light grey = Seagrass formation (modified from Bosire et al., 2003).

Mangroves in Gazi have been exploited for many years mainly as sources of fuel wood and building poles for the local community as well as to provide wood for brick and calcium industries in the 1970s (Kairo, 1995). Clear felling left some areas of the bay completely denuded (Bosire et al., 2003) and these sites still show few signs of natural regeneration. One of these cleared sites was used for the present study; it is a high tidal, sandy area, inundated only during spring tides (Figure 3.1). The three species used in this experiment grow sympatrically in the remaining natural forest contiguous to the experimental site and were present on the site before clear felling. Kenya has 9 mangrove species; top shore locations such as the study site commonly have 1-4 species.

3.2.2 Experimental design

The effects of mangrove species identity and richness, as well as of environmental variables, on aboveground biomass were investigated in a replanted area of 2800 metres^2. Three species of mangrove, *Avicennia marina, Bruguiera gymnorrhiza* and *Ceriops tagal* were used in the experiment. The eight treatments consisted of each species on its own, all two species mixes, the three species mix and unplanted control plots. In two and three species plots, saplings of various species were planted in alternate patterns in a regular matrix along the lines. Plots were 6×6 m^2, with a planting distance of 0.6 m between trees, hence each planted plot consisted of 121 trees, giving 3,388 trees in total. Inter-plot distances were kept to a minimum of 6 m; this is greater than the home range size of fiddler crabs (*Uca* spp) the dominant epifauna at the site, hence helping to ensure independence of plots (Skov et al., 2002). Treatments were randomly allocated to plots in a replicated random block design, with two blocks (separated by ~100m), each block containing two replicates; hence there was a replication of four plots for each treatment, and a total of 32 plots. Seeds and propagules of the three species were collected from the surrounding forest in early 2004 and grown in nursery plots using local soil with no artificial fertilizer application. They were subsequently planted in the treatment plots in July/August 2004. All planted saplings were ~30cm in height, of the same age, and were randomly allocated to relevant plots.

3.2.3 Environmental factors

The following environmental variables were measured in all plots before planting: a) redox potential, b) pore water salinity, c) sediment organic carbon content, d) sediment grain size, e) sediment temperature f) nutrient content and g) height above sea level. Areas <1.0 m from plot edges were not sampled to avoid 'edge effects'. For variables a)-f) the results for each plot were means of four random sub-samples; height above sea level was measured in the centre of each plot using a levelling theodolite. Sediment cores for redox and salinity measurements were extracted using a 50cm long, 40mm diameter D-section soil corer. A portable redox meter was used to take redox measurements in the extracted core at 10cm and 40 cm; ~50g sediment per depth was then removed, bagged and the pore water salinity measured in the laboratory after centrifuging, using a hand-held refractometer. Surface scrapes (to 1 cm depth) were taken for grain size and carbon analysis; the percentages of silt and coarse sand in surface scrapes were calculated following manual sieving over 65 and 500 μm mesh, and the percentage carbon was calculated as loss on ignition at 480°C. Surface temperature (probe inserted to 1 cm below sediment surface) was measured at midday on a clear sunny day. Sediments for nutrients analysis were collected in the field and preserved in an ice box before being taken to the laboratory. Lab nutrient extraction was done using Potassium chloride flashed with nitrogen gas (2 minutes) and shaken for 2 hours, to ensure maximum extraction. The sample was then centrifuged at a speed of 2000x g.r.m. for 10 minutes. The extract was decanted and diluted with distilled water and used for the determination of nutrients. Ammonium, nitrate and phosphorus were determined according to Parsons et al. (1984).

3.2.4 Sapling aboveground biomass and leaf growth

In order to non-destructively monitor the aboveground biomass of planted trees we developed biomass to tree-size regression equations for each species, using wild trees of representative sizes: Twenty five, 18 and 8 saplings of *A. marina, B. gymnorrhiza* and *C. tagal*, respectively, with stem diameters ranging from 2 to 22 mm, were selected in an area adjacent to the plots. Tree height, from the ground to the point where top-most set of leaves join the stem (apical bud), and stem diameter at 30 cm (*A. marina*), or between the 1st and 2nd internode (*B.gymnorrhiza* and *C. tagal*), were recorded using tape measure and calipers, respectively, and subsequently the saplings were cut at ground level. Saplings were weighed on site and subsequently oven-dried at 80°C to constant weight to determine fresh weight to dry weight ratio. An equation of the form $Y=ab^x$ was developed using the best predictor available to allow estimation of sapling biomass for planted trees of each species.

Aboveground biomass in plots was measured in August 2005, 2006 and 2007. Eighteen plants were randomly selected in each plot. In plots with 2 or 3 species, stratified random sampling was used to give 9 or 6 plants per species respectively. Tree heights and stem diameters were measured as described above. The total number of leaves and the percentage yellow leaves (a sign of stress) on each of the selected plants were counted and ten leaves were further selected for measurement of leaf length and maximum width.

The leaf area index in each plot was calculated for each species in turn by multiplying the mean total number of leaves per tree by the mean area per leaf, and integrating this value with the number of surviving trees per plot. The mean area per leaf was derived from the ten leaf length-width measurements per tree (conversions of length-width measures into true leaf area was obtained from regression equations based on > 30 'wild' leaves).

3.2.5 Recruitment of wildlings

Mangrove trees recruit naturally by the establishment of propagules that have fallen to the ground from nearby trees, or which have been carried in by the tide. The total number, the status (living or dead) and the species of wildlings recruited to each plot were recorded in August 2005, 2006 and 2007.

3.2.6 Statistical analysis

Data were checked for normality and homogeneity of variances, and transformed where necessary. To ascertain whether the equations were species-specific or general, the allometric regression slopes (for relationships between aboveground biomass and stem diameter) for the three species were compared using homogeneity of slopes model test. Effects of year, blocks and treatments on aboveground biomass, tree height, % yellow leaves and leaf area index were analysed using repeated measures ANOVA; when significant year × treatment interactions were found, yearly samples were separated and re-analysed using mixed-model 2-factor ANOVAs. Year and block were treated as random factors and species treatments as fixed factors.

The 2007 data was explored to ascertain whether significant species richness effects were due to 'the selection effect' or 'the complementarity effect' following the method of Loreau and Hector (2001). The net effect was calculated as $\sum B-\bar{E}$, where B is the total biomass for each species in a plot. $\sum B$ is the biomass of all the species in a plot and $\bar{E}$ is the average monoculture biomass of all the species in that plot. The net effect was partitioned into two additive components: the selection effect and the complementarity effect. Selection was calculated as $D \times COV(E, \Delta RB)$, where D is the diversity (i.e. species number), E represents a species' average monoculture biomass and ΔRB is the difference between the observed relative biomass (B/E) and the expected relative biomass (1/D).

Complementarity was calculated as $\bar{E}\times D\times\underline{\Delta RB}$, where $\underline{\Delta RB}$ is the average ΔRB of all the species in a plot.

The relationships between initial environmental variables in plots (treated here as predictor variables) and aboveground biomass in 2007 were analysed using stepwise multiple regressions (with inclusion of dummy variables in the multiple regression) with alpha values for predictor entry set at 0.2. Forward and backward selection procedures were compared, and the best model was selected on the basis of the adjusted R square, Mallow C and VIF as diagnostics. All the analyses were performed using SAS® (used for selection R squared method) and Minitab® software.

3.3 Results

3.3.1 Biomass estimation

Stem diameter was the best predictor of sapling biomass for each of the three species, with r^2 values exceeding 0.64 in each case (Table 3.1). There was significant species influence ($F = 46$. $P = 0.048$, $n = 51$) and hence we used different equations to estimate aboveground biomass for each of the three species.

Table 3.1: Regressions used to predict total aboveground biomass (in grams dry weight) of individual mangrove saplings from stem diameter. These equations are applicable to a stem diameter range of up to 22 mm. Stem diameter was measured at 30 cm above the ground in *A. marina* and diameter between first two internodes in *B. gymnorrhiza* and *C. tagal*

Species	Equation	r^2	*P*	*n*
A. marina	$0.6896 \times \text{stem diameter}^{2.0095}$	0.93	<0.001	25
B.gymnorrhiza	$0.6494 \times \text{stem diameter}^{1.7132}$	0.64	0.002	18
C. tagal	$0.4112 \times \text{stem diameter}^{2.1032}$	0.94	<0.001	8

3.3.2 Trends in aboveground biomass and other growth parameters

Unsurprisingly, aboveground biomass values varied between years (DF=2, F=596.2 p<0.001; Figure 3.2a). However, growth in the first two years was slow, with significant differences in species richness only emerging in 2007. In 2005, the mean (±s.e) aboveground biomass per plot was 3516 g dw (±180.0) while in 2007 the aboveground mean value was 10207 g dw (±1022.4). Plots containing *Avicennia* had the highest biomass increment between the three years while plots containing a mixture of *Bruguiera* and *Ceriops* had the lowest aboveground biomass increment values (Figure 3.2a). There was a significant year × treatment interaction (DF=12, F=3.721, p<0.001), hence biomass data for each year were analyzed separately using two way ANOVAs. There were no treatment effects in 2005 and 2006, but there was a significant effect in 2007.

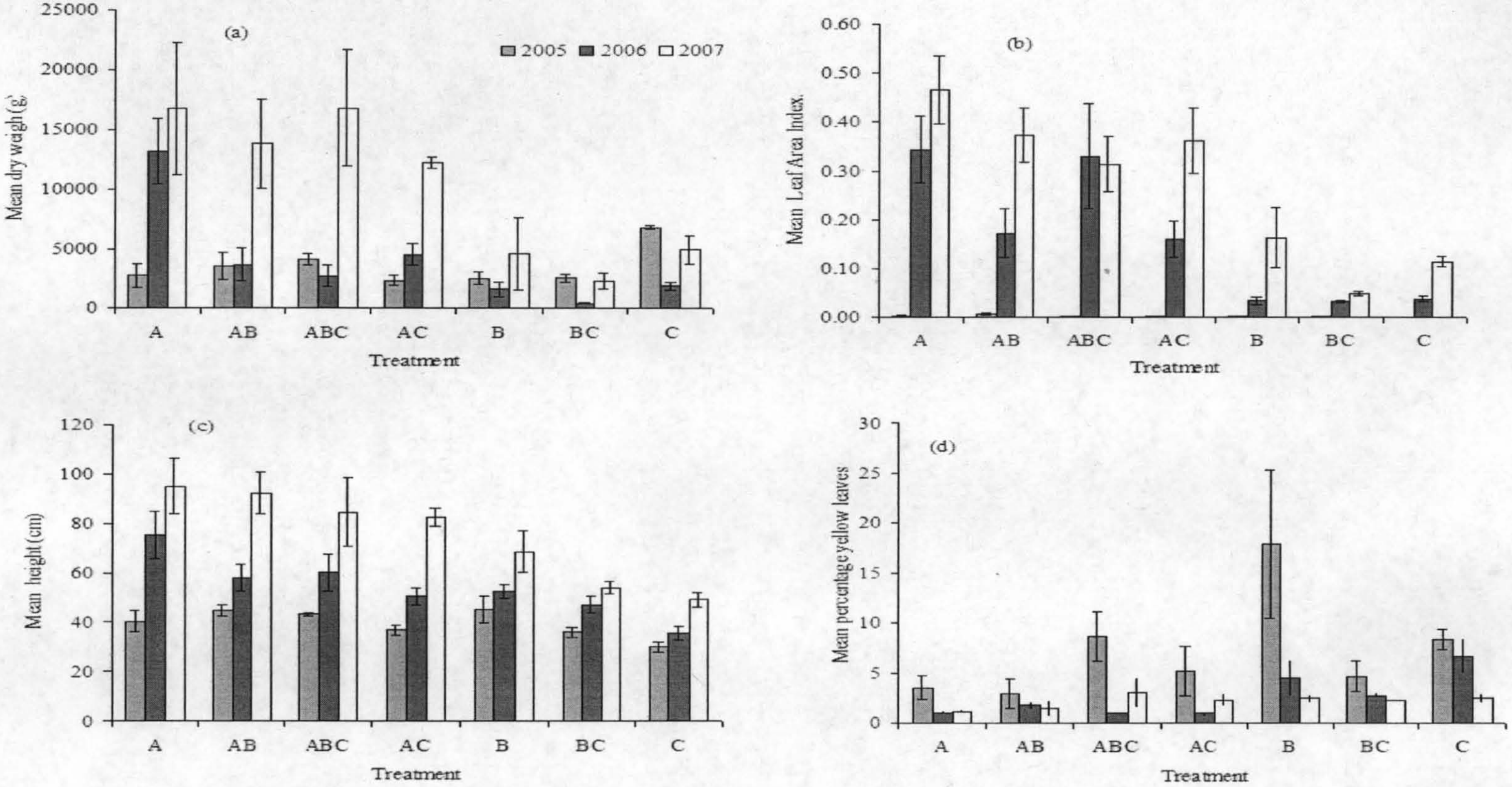

Figure 3.2: Mean (±s.e) growth parameters per 36m^2 plot per treatment (tree species richness) between the three years of the study: (a) aboveground biomass (b) leaf area index (c) tree height increment and (d) the percentage frequency of yellow leaves. A=*Avicennia*, B=*Bruguiera*, C=*Ceriops*.

Tree height showed a similar pattern, with a significant effect of year (DF=2, F=118.34 p<0.001; Figure 3.2c) as the mean tree height per plot increased from 39.6 cm (± 0.87) in 2005 to 75.4 (± 2.18) in 2007. There was a significant year × treatment interaction (DF=12, F=3.71 p=0.002).

There was a significant year effect on the mean leaf area index (DF=2, F=23.96, p<0.001; Figure 3.2b). Mean plot leaf area index in 2005 was 0.003 (± 0.0005) and had increased to 0.262 (± 0.046) by 2007. Again *Avicennia* exerted a strong influence, with plots containing *Avicennia* having a comparatively higher leaf area index (Figure 3.2b). However there was no significant year × treatment interaction (DF=12, F= 1.618, p=0.123). In contrast with biomass and height, there were significant differences in the leaf area indexes of treatments within all the three years. This may reflect the faster growth of leaves compared with overall biomass, which took longer to accumulate. There were significant differences between years in the frequency of yellow leaves (DF=2, F= p<0.001; Figure 3.2d). The highest frequency of yellow leaves was in 2005 at 7.3 % (± 3.7); this fell in the subsequent years to an average of 2.4 % (± 1.00) by 2007.

3.3.3 Aboveground biomass in 2007

There were significant treatment and block effects on aboveground biomass in 2007 (Table 3.2). Post hoc analysis (Tukey test) revealed treatments without *Avicennia* had significantly lower aboveground biomass values compared to A, AB, AC and ABC treatments; the mean aboveground biomass per plots with

Avicennia was 14000.9 g dw (± 0.29) compared to 3000.95 g dw (± 0.25) in plots without *Avicennia*.

Table 3.2: ANOVA table showing significance of the mean aboveground biomass (g dw/ 36m^2 plot) in blocks and between treatments in year 2007.

Source	DF	SS	MS	F	P
Block	1	5110.8	5110.8	7.45	0.016
Treatment	6	26828.4	4471.4	6.52	0.002
Interaction	6	4028.0	671.3	0.98	0.475
Error	14	9600.2	685.7		
Total	27	45567.5			

The highest mean aboveground biomass, of 16.79 kg (± 4.91), was recorded in the mixed species treatment containing all three species and the lowest (2.31± 0.69 kg) was recorded in the treatment containing *Bruguiera* and *Ceriops* (Figure 3.3).

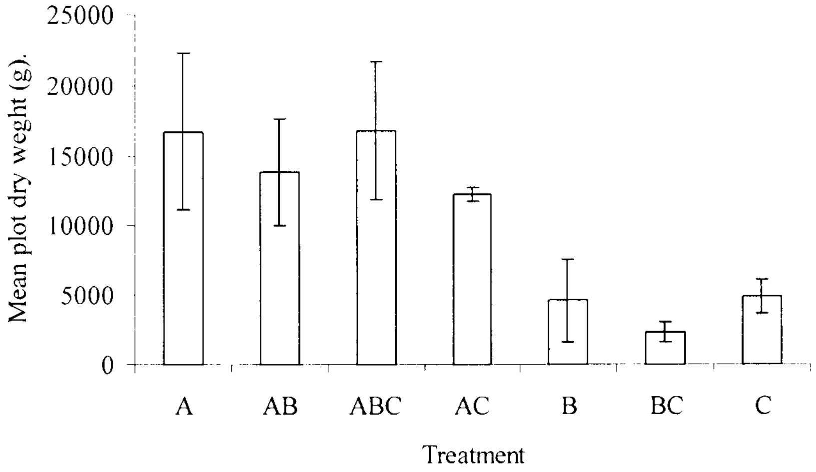

Figure 3.3: Mean (± s.e.) aboveground dry weights per 36m^2 plot in different tree-species treatments in 2007.

To explore the relative contributions of different species to the total plot dry weights, the mean dry weight per tree was calculated for each species, for each treatment that it was grown in. The average biomass of *Avicennia* individual trees was highest in the three species mix treatment and lowest in the monospecific treatment (Figure 3.4) with the difference approaching significance. However, aboveground biomass in *Bruguiera* and *Ceriops* did not differ significantly between treatments.

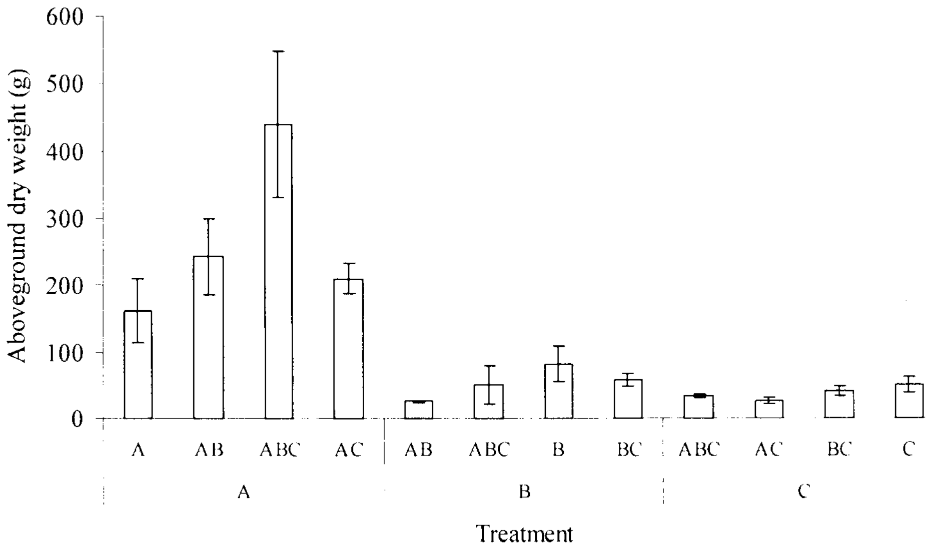

Figure 3.4: Mean (± s.e.) aboveground dry weights per 36 m^2 plot of each species in different species mixtures in 2007. *A = Avicennia, B = Bruguiera and C = Ceriops.*

There was a positive net richness effect resulting from mixing species, although this was marginal for two species mixes (Figure 3.5). Partitioning the net effect into the two components of selection and complementarity showed a strong selection effect. However, there was also positive complementarity in the three species plots (Figure 3.5).

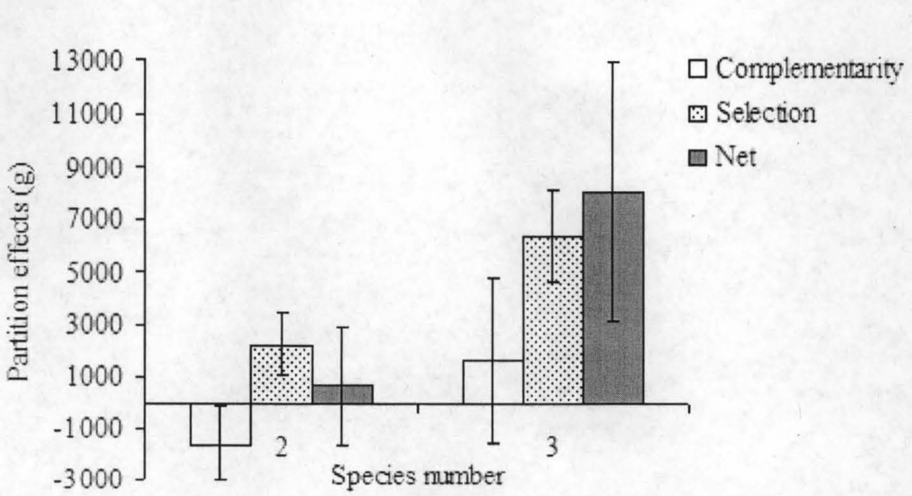

Figure 3.5: Complementary, selection and net species richness effects (±s.e) as functions of species number in the plots.

3.3.4 Height increment in 2007

Tree heights differed between treatments, (DF =6, F= 7.69, p= 0.013) and blocks (DF =1, F=6.69, p=0.041), but there was no treatment-block interaction. Plots containing *Avicennia* and a combination of *Avicennia* and *Bruguiera* differed from those containing only *Ceriops* and a combination of *Bruguiera* and *Ceriops* (Figure 3.2c).

3.3.5 Leaf area index 2007

There was a block effect (DF=1, F=11.33, p=0.015) and treatment effect (DF=6, F=6.99, p=0.016) on leaf area index. Tukey post hoc analysis showed the monospecific *Avicennia* treatment had a significantly higher index ($p=0.027$) than the mixed *Bruguiera* and *Ceriops* treatment.

3.3.6 Environmental variables

Twelve variables were examined for significant relationships with plot dry weight in 2007. These included the initial environmental factors and two dummy variables, block and *Avicennia* (presence or absence). The latter were included because of its obvious effects in the other analyses (running the test with inclusion of the other two species had no significant influence on the model); hence we intended to examine the importance of initial environmental variables separate from the influence of these factors. The best model included *Avicennia*, plot height above datum, sediment salinity and nutrient concentrations (ammonium and phosphates; Table 3.3). The regression involving these variables was highly significant (DF= 5, $r^2=0.86$, $p<0.001$) and was described by the equation:

Aboveground dry weight (g) = 1.00 - 0.012 salinity - 0.46 ammonium (µM/g) - 0.17phosphates (µM/g) + 0.61 *Avicennia* + 0.013 plot height (m)

Table 3.3: Results for multiple regressions showing coefficients for significant initial environmental variables on aboveground biomass. Nutrients are in µM/g, height above datum is in metres.

Variable	Coefficient	T	p
Intercept	1.00	0.56	0.58
Salinity	-0.012	-3.46	0.002
Ammonium	-0.46	-2.80	0.011
Phosphate	-0.17	-2.44	0.023
Avicennia	0.61	9.34	<0.01
Plot heights above datum	0.01	3.73	0.001

There was a positive relationship between aboveground biomass and *Avicennia* as well as plot height above datum, and a negative relationship between aboveground biomass and sediment salinity, ammonium and phosphates (Table 3.3).

3.3.7 Naturally recruited saplings (wildlings)

Few wildings were observed before 2007. In 2007, four species had recruited into the plots with *Ceriops tagal* predominating (92.1 %) reflecting the predominance of *Ceriops* in the vicinity. Other species recruited were *Rhizophora mucronata* (4.2 %), *Xylocarpus granatum* (3.3 %) and *Avicennia* *marina* (0.4%). There were significant treatment (DF =7, F=5.31 p= 0.02) and block (DF= 1, F=5.93, p=0.04) effects on wildlings recruitment (Figure 3.6). Plots containing the monoculture *Avicennia* treatment had the highest mean wildlings per plot (18 ± 11.44) whereas the control plot had the lowest mean wildling plants per plot (1 ± 0.41). The effects of *Avicennia marina* were apparent with the plots containing this species either singly or in combination with the other species having significantly higher numbers of recruited wildlings than the other treatments.

There were significantly different proportions of dead to living wildings between treatments (Figure 3.6). Data from treatments with, and from those without, *Avicennia* were pooled in order to avoid unacceptably low expected values in χ^2 analyses, and the two resulting distributions were compared. There was a significant difference (χ^2, DF =1, p=0.012), with a proportionately lower mortality in plots with *Avicennia* and a proportionately higher mortality in those plots (including unplanted controls) without *Avicennia*.

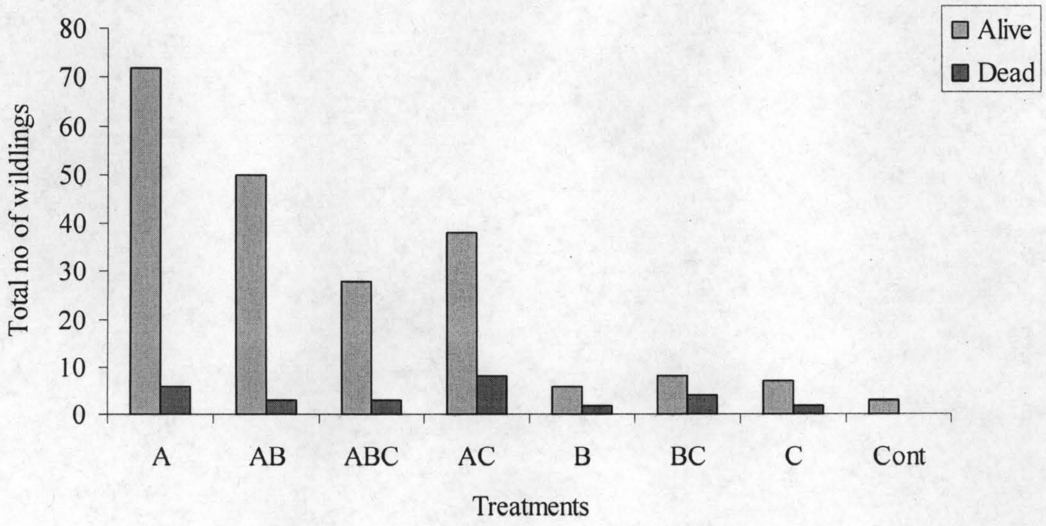

Figure 3.6: Total number of wildlings alive and dead recruited by 2007 into four $36m^2$ plots of each treatment. A=*Avicennia*, B=*Bruguiera*, C=*Ceriops*, Cont = control (no trees).

3.4 Discussion and Conclusion

There was a significant treatment effect on aboveground biomass, mean tree height and leaf area index three years after establishment. Results show evidence of a positive relationship between aboveground biomass and species richness, with a net effect of species mixing on biomass and the highest mean value recorded from the three species treatment. However, while there was evidence for species complementarity (Figure 3.5), it is clear that, at this relatively early stage in the growth of these plants, the 'selection effect' of the inclusion of the most vigorous species at our site, *Avicennia*, is the dominant contributor to the net effect observed. Such an effect has been inferred in earlier studies on a variety of marine ecosystems (e.g., Emmerson and

Huxham, 2002; Callaway et al., 2003; Bruno et al., 2005) and was invoked as a mechanism linking biodiversity and ecosystem function through the species selection effect in experiments on grassland ecosystems in earlier studies (Tilman and Downing, 1994; Tilman et al., 2001; Tilman et al., 2006).

Plots with *Avicennia* tended to show the fastest growth rates, the highest mean heights, the greatest leaf area indices and the lowest Percentage yellow leaves. The relative success of *Avicennia* reflected its inherent wide tolerance range to salinity and aridity as exhibited at the experimental site (Kirui et al., 2008). Vegetation cover loss following removal of the initial forest cover at the field site had led to salinisation of the sediment and a total lack of natural regeneration; under these conditions, it was necessary to plant nursery-reared trees to initiate restoration, and our results suggest *Avicennia* acts as a 'superplant' (Zedler et al., 2001) in fostering ecosystem recovery. These results are concordant with the findings in some terrestrial grassland (Hooper and Dukes, 2004, Hooper et al., 2005), freshwater plant, microbial (Downing, 2005; Bruno et al., 2006), and salt marsh communities (Callaway et al., 2003) that showed that productivity was driven by a species identity effect.

In biodiversity-productivity experiments, a positive relationship between monoculture biomass and the relative yield of a species in mixture is predicted to result in 'positive selection' caused by a sampling effect (Fargione et al., 2007); such a relationship is seen in the current work with *Avicennia* performing best in monoculture and acting as a competitive dominant in polyculture.

However, recent metaanalysis by Cardinale et al. (2007) and work by Fargione et al. (2007) showed that positive selection effects predominated early during their ten year grassland experiment, with the effects of complementarity between species increasing over time. Hence complementarity may emerge more strongly in the current work in subsequent years.

The mean aboveground biomass of individual *Avicennia* trees was highest in plots containing the three species combination and lowest in monospecific plots (Figure 3.4). These differences were probably caused by interspecific competition for resources. In single species plots, *Avicennia* plants were competing against one another. In three species combination plots, the relatively poorer growth rate of the other two species resulted in less competition and hence greater individual growth for *Avicennia*.

In addition to the strong influence of *Avicennia*, initial environmental variables in plots also affected plant growth. There was a significant positive correlation between tree biomass and plot height above datum, and a negative correlation with sediment salinity, ammonium and phosphates. While salinity has been widely reported as a factor limiting growth (e.g. Naidoo, 1990), the negative effects of ammonium and phosphates came as a surprise. However, Saenger (2002) reported that low sediment nitrogen conditions negate the influence of phosphorous on plant growth, and we recorded very low average nitrogen levels of 31.69 µM/g (±14.33). Ammonium and phosphate may correlate with factors such as oxygen availability in the sediment. Although we found no significant effects of sediment redox, this was highly variable between and within plots (perhaps because of the remains of roots from the previous forest on the site). Hence we may not have captured the importance of sediment oxygen status, and the ammonium and phosphate could be acting as surrogates for this. Sherman et al. (2003) reported a negative correlation between ammonium and aboveground biomass which they attributed to the influence of salinity on soil exchange processes where sodium ions replaced ammonium.

The positive effect of height above chart datum on biomass was also unexpected. This remained in the model despite the inclusion of block as a variable; there were large differences in growth performance between blocks, and the blocks differed in their average heights. Whilst the total range in plot heights was small (3.14m - 3.42 m), and thus all plots were at virtually the same tidal level, it is possible that plots at slightly lower elevations suffered from 'puddling' effects after tidal retreat (stagnant, shallow puddles of seawater), which could have reduced oxygen and increased salt in these plots.

Avicennia exerted a strong influence on the probability of the establishment of wildings in a plot. Two mechanisms may be responsible; first, the network of *Avicennia marina* pneumatophores may have facilitated settlement by physically trapping propagules. Second, given the superior growth and survival characteristics of *Avicennia* at this site, the trapped propagules may have benefited from the impacts of *Avicennia* on the microhabitat within the plots, in particular greater shading and increased sediment moisture and nutrients (Kirui et al., in prep). Our results suggest both mechanisms were operating, with significantly higher numbers of wildings establishing and significantly lower proportions of them dying, in plots with *Avicennia* (Figure 3.6). The amelioration of abiotic stressors such as high temperature, hypersalinity and drought conditions by pioneer/ superior species has been inferred in salt marsh and grassland communities (Callaway, 1995; Greenlee and Callaway, 1996; Zedler et al., 2001; Bertness and Ewanchuk, 2002) where this process is thought to facilitate secondary succession. Bosire et al. (2003) found significant differences in the number of wildlings recruiting to bare areas and reforested and natural mangroves areas, possibly because of similar effects. Milbrant and Tinsley (2006) reported significantly enhanced survival of *Avicennia germinans* seedlings planted in patches of saltwort (*Batis maritima)*. They explained this facilitative effect as arising from marginal elevation of the sediment by the *Batis* roots. Our work concurs with these studies in finding facilitation of mangroves by larger trees, and extends them by demonstrating this with a fully randomised experiment that is not confounded by possible pre-existing within-site variability.

In conclusion, above-ground productivity over the three years of our study was driven by the presence of *Avicennia*, which was the competitively dominant species at our site. This was probably because of its tolerance of salt (which showed a strongly negative association with productivity) and other environmental stressors. There was some evidence for complementarity between the trees planted in the experiment, and there was a significant facilitation effect of our planted trees, particularly *Avicennia*, on the recruitment of wild seedlings, nearly all of which were *Ceriops tagal*.

Acknowledgement

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References

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CHAPTER 4: BELOWGROUND BIOMASS IN REPLANTED MANGROVES: EFFECTS OF SPECIES RICHNESS, IDENTITY AND ENVIRONMENTAL FACTORS ON ROOT ACCUMULATION

Based on: Kirui, B., Tamooh, F., Langat, J., Huxham, M., Kairo, J., Skov, M. and Mencuccini, M. Tree root biomass allocation in replanted mangroves; effects of species richness, identity and environmental factors. (Manuscript).

CHAPTER 4: BELOWGROUND BIOMASS IN REPLANTED MANGROVES: EFFECTS OF SPECIES RICHNESS, IDENTITY AND ENVIRONMENTAL FACTORS ON ROOT ACCUMULATION

Abstract

Root biomass represents a significant proportion of net primary productivity. However data on belowground biomass is scant and is mostly based on findings from studies conducted in terrestrial forest. Due to their unique location where the substrate is unstable and there is presence of wave action, mangrove forests allocate a significant proportion of their photosynthate to the belowground components. We investigated the influence of species richness and environmental variables on root biomass allocation, and root: shoot ratios in young replanted mangroves. Results reveal significant differences amongst species regarding root biomass allocation and root: shoot ratios three years after planting. Plots with *Avicennia marina* exhibited higher mean-plot root biomass values as well as root: shoot ratios compared to other plots. Salinity and ammonium were negatively correlated with root biomass while percentage silt and nitrates were positively correlated. Salinity was negatively correlated with root: shoot ratio. Interspecific differences in root biomass allocation and root: shoot ratios become apparent at a much earlier stage in mangrove tree growth. Also sediment salinity levels have a major bearing on the pattern of photosynthate allocation.

Keywords: Belowground, biomass, Mangroves, root: shoot ratio.

4.1 Introduction

Root biomass production represents a significant proportion of total annual net primary productivity (NPP) in most forest ecosystems; globally 33 % of annual NPP is estimated to be used for the production of fine roots (Jackson et al., 1997). Ecosystem processes such as nutrient cycling, nutrient storage, soil production, and sediment vertical accretion are largely controlled by the rhizosphere (Trumbore and Gaudinski, 2003). In spite of the importance of rooting system, most biomass studies in forestry have focused on aboveground components (e.g. Cairns et al., 2003; Santos et al., 2003; Sah et al., 2004 Dias et al., 2006). Reports from terrestrial forest indicate belowground biomass contribution to represent less than 30% of the total biomass (Sanford and Cuevas, 1996; Vogt et al., 1996) but this figure may not be relevant to mangroves. Mangroves differ from terrestrial forests in many ways, including in the physiology and ecology of their rooting systems (e.g. Komiyama et al., 1987). Mangroves have two general types of roots: aerial roots, which occur above the soil surface and provide a pathway for oxygen entry, and roots that grow in the anaerobic soil (McKee, 1996).

As in terrestrial forests, root processes are important to mangrove ecosystem productivity and nutrient dynamics. In addition, and of unique importance to mangroves, root production and decomposition determine the ability of the vegetation to effect changes in soil height, and thus potentially accommodate sea-level rise (Chmura et al., 2003, McKee et al., 2007). There are few estimates available for belowground biomass in mangroves partly due to the logistical difficulties in obtaining them. Most relevant studies suggest that belowground biomass may represent 10-55 % of the total biomass (e.g. Komiyama et al., 1987; Gong and Ong, 1990; Saintilan, 1997a; Komiyama et al., 2000; Alongi et al., 2003, Sherman, 2003; Comley and McGuiness, 2005) hence understanding below-ground processes is crucial in understanding mangrove forest dynamics in general.

Biomass partitioning between different parts of the trees has been shown to vary with forest age, forest structure, competitive interactions and environmental conditions (Clough, 1992). Komiyama et al. (1987) reports increasing biomass allocation to root biomass with decreasing tidal inundation suggesting a response to stressful conditions such as higher salinity which generally increases the root/shoot ratio (Saintilan, 1997a; Sherman et al., 2003). High salinity has been shown to increase the carbon cost of water uptake, which might reflect an increase in root: shoot ratio along gradients of increasing soil salinity (Soto, 1988; Saintilan, 1997a, 1997b). Mangroves experience predictable hydroperiods due to tidal flooding, but the tidal regime may vary substantially among mangrove forest types (Lugo and Snedaker, 1974). Such differences in hydrology have been shown to influence salinity levels, nutrient availability, and sulfide concentrations with effects on mangrove aboveground productivity (Day et al., 1982; Twilley et al. 1986; Chen and Twilley, 1999). However, there is a lack of information on the effects of hydrology on the belowground dynamics of mangroves. Experimental studies (Onuf et al., 1977) and surveys (Naidoo, 1990; McKee, 1995; Feller et al., 1999; Feller et al., 2002; Feller et al., 2003; Lovelock et al., 2004) in mangroves have found that mangrove growth and productivity may be controlled by nutrient limitations of either nitrogen (N) or phosphorus (P) or both nutrients depending on local or regional characteristics. However, gaps in knowledge exist on root allocation and growth rates. In particular, there is a lack of controlled studies comparing different species in the same place i.e. without major confounding from shoreline gradients and related variables.

There are few studies on biomass allocation among young mangrove plants. Snedaker (1995) reports that young plants tend to allocate more biomass to the roots, a condition which is reversed as the tree matures. Naidoo (1990) analyzed the effects of nitrate, ammonium, and salinity on the growth of *Bruguiera gymnorrhiza*. He found that at low salinity, N additions increased biomass accumulation especially aboveground (total, leaves, and stems dry mass), yielding a greater shoot/root ratio. However these studies were mostly based on surveys where there were no controls on potential confounding environmental factors e. g. shoreline gradients. In this study we used three species and experimentally manipulated species richness and measured a range of environmental and biotic responses including belowground biomass allocation.

Increasing concerns over the consequences of reduced species diversity on ecosystem functions emphasise the need for quantitative information on the value of diverse systems. Several experiments have been conducted testing the relationship between species richness and ecosystem functions. In most cases, aboveground biomass productivity has been used as a surrogate for ecosystem functions (e.g., Spehn et al., 2000; Cox et al., 2006), although a few studies have reported on the potential effects of species richness on belowground biomass in grassland ecosystems (Kahmen et al., 2005).

In July 2004, a long-term experiment measuring a range of ecosystem functions was established at Gazi bay in Kenya. The experiment used three species (*Avicennia marina, Bruguiera gymnorrhiza and Ceriops tagal)* growing sympatrically near the experimental site to create treatments containing all possible species combinations. Early findings on the effects of species diversity and identity on root biomass and distribution are presented. Description of the productivity and vertical distribution of roots of different species and species mixes as well as comparison with root biomass from an adjacent naturally growing mangrove stand is made. The following null hypotheses were tested:

1) Species diversity does not influence root: shoot ratios and root biomass

2) The stand root: shoot ratios and root biomass are unaffected by environmental factors including soil redox and salinity.

4.2 Materials and Methods

4.2.1 Study area

Gazi Bay (4.92°S, 39.50°E; Figure 4.1) is a shallow tropical coastal water system located on the southern coast of Kenya, approximately 50 km south of Mombasa. The mangrove forest covers a surface area of about 7 km^2 (Kitheka, 1997) The bay is drained by two main rivers, the River Kidogoweni on the north-west part of the bay and the River Mkurumudji on the south-west side of the bay.

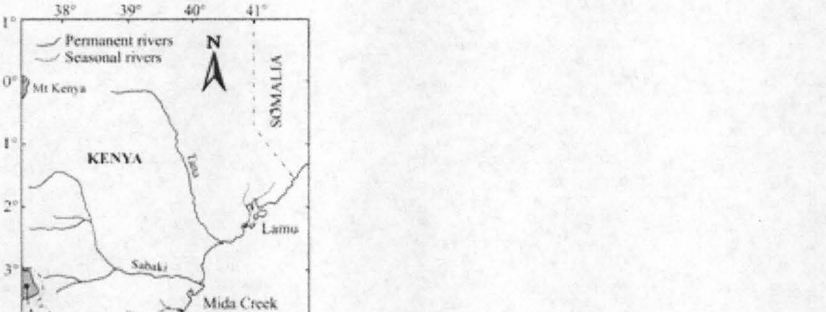

Figure 4.1: Map of the study area (modified from Bosire et al., 2003)

The tides in the bay are mainly semi-diurnal with a tidal range of 3 m (Kitheka, 1997). The maximum current velocities are of the order of 0.6 m sec^{-1} in the narrow creek sections in the upper zone but are much lower in the broad and shallow lower sections of the bay, about 0.3 m sec^{-1}.

4.2.2 Experimental design

The effects of mangrove species identity and richness, as well as of environmental variables, on root biomass were investigated in a replanted area of 2800 $metre^2$. Three species of mangrove, *Avicennia marina, Bruguiera gymnorrhiza* and *Ceriops tagal* were used in the experiment. The eight treatments consisted of each species on its own, all two species mixes, the three species mix and unplanted control plots. Plots were 6×6 m^2, with a planting distance of 0.6 m between trees, hence each planted plot consisted of 121 trees, giving 3,388 trees in total. Inter-plot distances were kept to a minimum of 6 m; this is greater than the home range size of the fiddler crab (*Uca* spp), the dominant epifauna at the site, hence helping to ensure independence of plots (Skov et al., 2002). Treatments were randomly allocated to plots in a replicated random block design, with two blocks (separated by ~100m) each containing two replicates; hence there was a replication of four for each treatment, and a total of 32 plots. Seeds and propagules of the three species were collected from the surrounding forest in early 2004, and grown in nursery plots before planting in the treatment plots in July/August 2004.

Transplanted saplings were of ~30cm in height, of the same age, and were randomly allocated to relevant plots.

4.2.3 Root biomass sampling

Root samples were collected using soil cores (internal diameter. = 5 cm). Each treatment plot was divided into four parts and in each quarter two random cores were collected to a depth of 40 cm giving a total of 8 samples per plot. Samples were separated into different sediment depths (0-10 cm. 10-20 cm, 20-30 cm and 30-40 cm) and placed in tight bags before being taken to the laboratory where they were washed and separated into different root sizes (large: >2.5mm diameter and small: < 2.5mm diameter). Wet weights of root samples were obtained before they were oven dried at 80°C for 48 hours after which their dry weights were obtained. Data from the aboveground components (sampling method elaborated in Chapter 3) was used together with the root biomass data to obtain root: shoot ratios

4.2.4 Environmental variables

The following environmental variables were measured in all plots before planting: a) redox potential, b) pore water salinity, c) sediment organic carbon content, d) sediment grain size, e) sediment temperature f) nutrient concentrations and g) height above sea level. Areas <1 m from plot edges were not sampled to avoid 'edge effects', and for variables a)-f) results for each plot were means of four random sub-samples; height above sea level was measured in the centre of each plot using a levelling theodolite. Sediment at 10 cm and 40 cm depths was obtained for redox and salinity measurements using a D-section soil corer. A portable redox meter was used to record redox measurements; pore water salinity was measured by taking approximately 50g sediment for centrifuging in the laboratory to extract pore water for salinity measurements using a hand-held refractometer. Surface scrapes (to 1 cm depth) were taken for grain size and carbon analysis; the percentages of silt and coarse sand in surface scrapes were calculated following manual sieving over 65 and 500 μm mesh, and the percentage carbon was calculated as loss on ignition at 480°C. Surface temperature (probe inserted to 1 cm below sediment surface) was measured at midday on a clear sunny day. Sediments for nutrients analysis were collected in the field and preserved in an ice box before being taken to the laboratory where nutrient extraction was done using potassium chloride flashed with nitrogen gas (2 minutes) and shaken for 2 hours, to ensure maximum extraction. The sample was then centrifuged at a speed of 2000x g.r.m. for 10 minutes. The extract was then decanted and diluted with distilled water and used for the determination of nutrients. Ammonium, nitrate and phosphorus were determined according to the procedure of Parsons et al. (1984).

4.2.5 Statistical analysis

Data were tested for normality and homogeneity of variance and transformed (square root or log) where necessary. Variations in root biomass and root: shoot ratio between blocks, treatments and at different sediment depths were analyzed using general linear model ANOVAs with interactions and post-hoc analysis performed using Tukey test. The effects of environmental variables on belowground biomass were explored using multiple regressions. All analyses were performed using Minitab V14 package.

4.3 Results

4.3.1 Root biomass

Root biomass per plot was calculated from the pooled biomass in the 8 cores. There was low root biomass in the plots and hence for the purpose of analysis we pooled together the fine roots and the coarse roots. We found significant block effect (ANOVA, DF = 1 $p = 0.03$), species richness effect (ANOVA, DF = 6 $p = 0.01$; Figure 4.2) and depth effect in the root biomass distribution (ANOVA, DF = 3 $p < 0.001$). However there was no block × treatment interaction. Post hoc analysis on treatment effect revealed significant differences in root production between the following treatments: monospecific *Avicennia* and mixed *Avicennia*, *Bruguiera* and *Ceriops* were significantly higher than from plots of

Bruguiera (p = 0.02), mixed *Bruguiera* and *Ceriops* (p = 0.01) and mono *Ceriops* treatment (p = 0.01). Across all the treatments, total root biomass ranged from 0.011 g m^{-2} to 0.67 g m^{-2} with a mean of 0.25 ± 0.22 g m^{-2}. Root biomass values were highest at 10-20 cm sediment depths (4068 ± 1929.64) g and lowest at 30-40 cm sediment depths (580.0 ± 347.6) g.

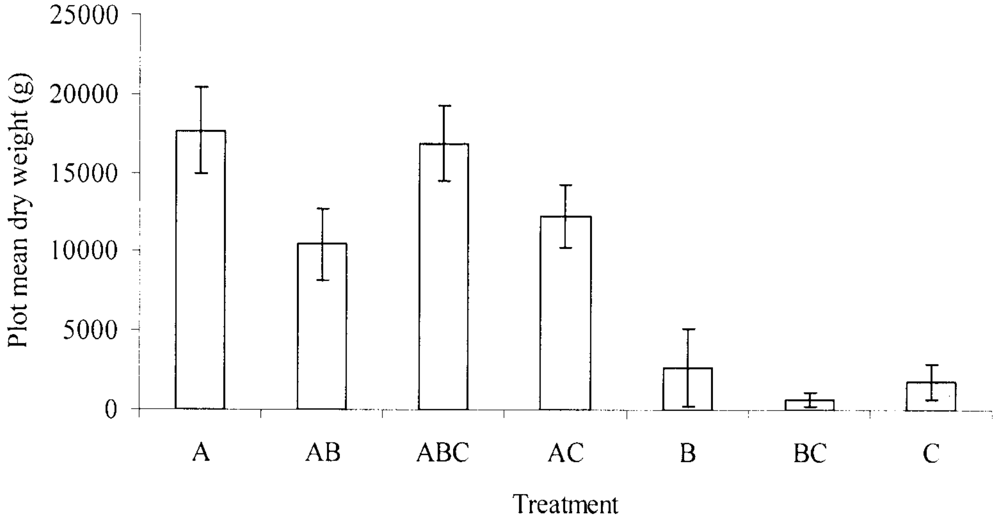

Figure 4.2: Mean (±s.e.) root biomass (g dw/ 36m^2 plot) of different treatments. *A = Avicennia, B = Bruguiera, C = Ceriops*

Separately, scrutiny of individual categories of roots (coarse and fine) showed that coarse roots had the highest contribution to total root biomass (> 60 %) in all the plots except in plots with *Bruguiera* × *Ceriops* combination which had a higher fine root contribution (Table 4.1). Treatments containing *Avicennia* generally had higher percentage coarse roots (>80) than other treatments.

Table 4.1: Mean (± s.e) percentage contribution of coarse and fine roots to the total root dry weight

Treatment	% Coarse roots (>2.5mm)	% Fine roots (<2.5mm)
A	83.45±3.79	16.56±1.90
AB	79.71±9.68	20.29±4.84
ABC	85.21±5.37	14.79±2.69
AC	83.41±6.53	16.59±3.27
B	65.94±44.81	34.06±22.40
BC	76.44±23.56	23.56±47.13
C	79.81±26.75	20.20±13.38

4.3.2 Stand root: shoot ratio.

Stand root: shoot ratio ranged from 0.02 to 1.57 with an overall mean of 0.73 ± 0.25 across the treatments. There was a treatment effect (ANOVA, DF= 6, p=0.039; Figure 4.3). An *Avicennia* species identity effect was apparent in the root:shoot ratios with high ratios of >1 being observed in plots containing *Avicennia* (Figure 4.3) and the rest of the treatment plots generally recording low root: shoot ratios of less than 0.5 (Figure 4.3).

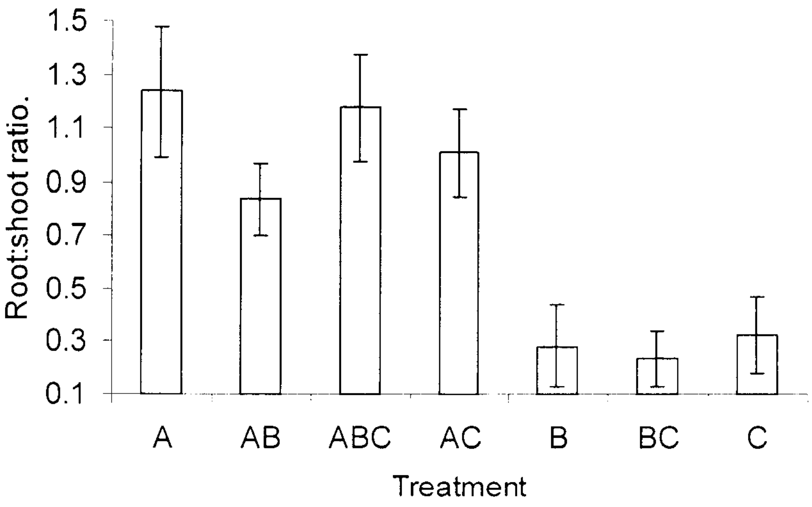

Figure 4.3: Mean (± s.e) root: shoot ratios across the eight treatments. A = *Avicennia, B = Bruguiera, C = Ceriops*

The relationship between three key environmental variables (i.e. nitrates, phosphates and salinity) and root: shoot ratio was analysed using regressions. Increasing salinity levels led to significant reduction in root shoot: ratios (Figure 4.4a). High nutrients and phosphate levels led to reduction in root: shoot ratio as well though the effects were not significant (Figures 4.4b and 4.4c).

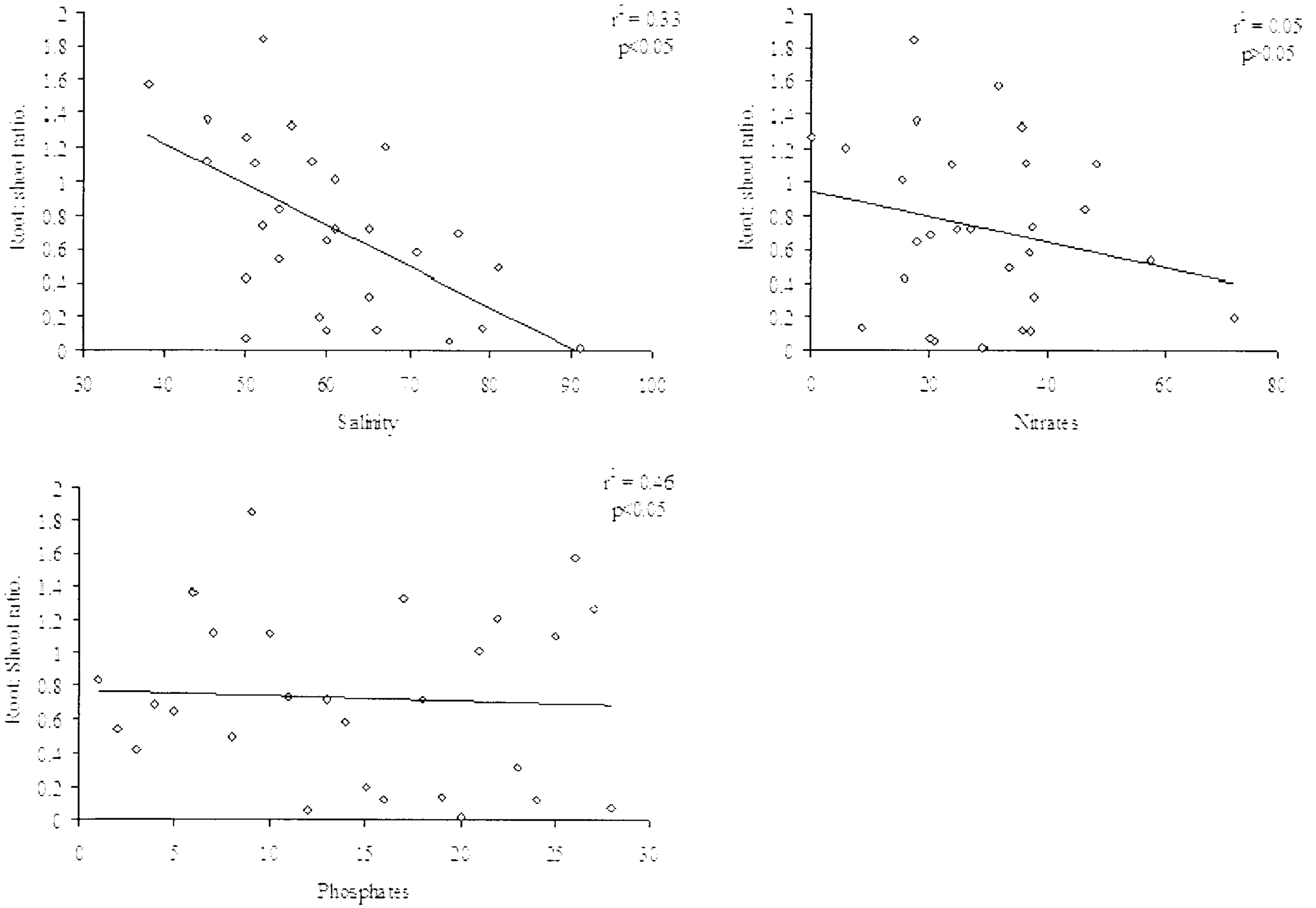

Figure 4.4: Relationship between root: shoot ratio and a) salinity b) nitrates (μM/g) and c) phosphates (μM/g).

4.3.3 Environmental variables

Twelve variables were used to examine the influence of environmental conditions on belowground biomass. These included *Avicennia* presence or absence as a dummy variable given its major influence on a range of responsive variables (Inclusion of the other two species did not affect the influence of environmental variables on belowground biomass). The best equation developed included *Avicennia*, salinity, nitrates, % silt and ammonium. The regression equation was highly significant (DF=5, r^2=0.87, p<0.001,) and is described as:

Biomass= 1877+1015 *Avicennia* - 23.5 salinity + 45.7 % silt +10.2 nitrates (µM/g) – 643 ammonium(µM/g)

There were positive relationships between belowground biomass and % silt, nitrates and *Avicennia* and a negative relationship with salinity and ammonia (Table 4.2).

Table 4.2: Results for multiple regressions showing coefficients for significant initial environmental variables on belowground biomass

Variable	Coefficient	T	P
Intercept	1877	2.45	0.023
Avicennia	1015	8.69	<0.001
Salinity	-23.5	-4.99	<0.001
% Silt	45.7	3.05	0.006
Nitrates	10.2	2.62	0.016
Ammonium	-643	-2.30	0.032

4.3.4 Comparison of root biomass of *A. marina* in natural and replanted stands

Comparison of root biomass allocations by *Avicennia* at two adjacent stands - a 12 year old *Avicennia* plantation and a natural forest - with the belowground biomass values in our plots (Table 4.3) was made. At all three sites, the highest biomass values were found in the top 20 cm depth and with lower values at greater depths.

Table 4.3: Percentage root biomass at different depth in this study and in a 12 year stand and a naturally growing plantation

Depth (cm)	(This study)	(12 year plantation)*	(Naturally growing plantation)*
0-20	79.9	54.3	51.3
20-40	20.1	26.1	38.5
40-60	-	19.5	10.3

- Source: Tamooh et al. (in preparation)

4.4 Discussion and Conclusion

There were generally low biomass values in the plots due to the young age of the trees and slow growth rates. It became difficult to separate the roots obtained into coarse and fine compartments hence we pooled the data for both categories for statistical analyses. Species richness effect on root biomass was apparent with high mean plot values being recorded in plots containing *Avicennia marina* (due to the extensive underground cable system) thus supporting earlier findings which showed a large influence of *Avicennia* on survival, aboveground biomass and wildling recruitment into these plots and thus suggesting a strong *Avicennia* species identity effect on ecosystem functioning at this site. Unfortunately it was not possible to reliably distinguish between roots of the three species, and so we cannot partition the effects of species mixing into selection (caused by the presence of *Avicennia)* and complementarity in the mixed species plots. The relatively large root biomass recorded in the mixed species plots containing *Avicennia* is probably to do with inherent high growth rate of the species. The maximum annual increment (MAI) in height for replanted *Avicennia* in Gazi has been estimated at 1.1 m/yr (Kairo et al., 2001); compared to *Bruguiera* and *Ceriops* whose maximum annual increment rates are 0.8 and 0.3 m/yr respectively. While information on species identity effects on root biomass in mangroves is scant, experimental findings showing strong species identity effects in aboveground productivity have been reported for coral reef macroalgal communities (Bruno et al., 2005, 2006), terrestrial plants (Hooper, 2005), freshwater plants (Engelhardt and Ritchie, 2002; Downing 2005) and salt marsh communities (Callaway et al., 2003).

Root production in this study varied between different species monoplots and mixed species plots (Table 4.4).The pattern observed in root biomass where *Avicennia marina* performance was higher compared to the other species was also evident in root production. Comparisons with global estimates reveal that the root estimates in this study were lower than the reported values from other areas of the world (Table 4.4). However, the variation in stand age as well as in methodologies may explain the observed discrepancies.

Table 4.4: Estimates of root production in this study and from global sources

Author	Location	Community	Root production g m^{-2} yr^{-1}
McKee and Faulkner 2000	Florida	Basin	18-1146*
Cahoon et al., 2003	Honduras	Fringe	311*
		Basin	333*
Giraldo-Sanchez, 2005	Florida	Fringe	352*
		Basin (mixed)	314*
		Basin (mono)	378*
		Scrub	307*
This study	Gazi bay	Plantation (*Avicennia*)	40.9
		Plantation(*Bruguiera*)	14.2
		Plantation (*Ceriops*)	8.1

* Estimation based on root in-growth core technique

While some mangrove species are capable of extending their root system to as deep as 1 metre most root biomass is concentrated in the upper part of the soil profile (Komiyama et al., 1989). In this study, root biomass was highest at the top 20 cm and gradually declined with depth, studies done in adjacent natural vegetation and in 12 year old stands had high root biomass concentration in the 20-40 cm soil depth profile (Table 4.3).

Belowground biomass increased under silt conditions and at high nitrate levels but decreased as salinity and ammonium levels went up. Positive influence of nitrates on root biomass has been reported in a number of studies (e.g. Naidoo, 1990; Giraldo-Sanchez, 2005). The negative correlation observed between belowground biomass and ammonium may be explained by the influence of salinity on soil exchange processes (Sherman et al., 2003). Boto et al. (1985) reports that prolonged exposure to ammonium ions in the absence of nitrates led to marked reduction in growth and eventual death of *Avicennia marina* seedling. Studies have shown that high salinity (Kirui et al., in press), high soil sulfide concentrations (McKee, 1993), low soil redox potentials (Pezeshki et al., 1990; McKee, 1993), flooding frequency and duration (Ellison and Farnsworth, 1997), and low-nutrient conditions (Lin and Sternberg, 1992; McKee, 1995) all can negatively affect mangrove seedling growth and, in some cases, increase C allocation to roots. Thus, it appears likely environmental stress factors are acting in combination with salinity to influence growth and root allocation at our plots.

There were variations in environmental effects between aboveground biomass and belowground roots. For instance, nitrates and percentage silt effects were apparent in belowground biomass but absent in aboveground biomass. There is need therefore to include belowground biomass in understanding what controls tree biomass allocation. For instance (Kahmen et al., 2005) reports increasing species diversity in semi-natural grasslands to enhance belowground productivity during drought periods while aboveground biomass remained independent of plant diversity.

Root production, root biomass and root: shoot ratio values in this study were generally low and showed variation with species. This indicates that three year after plantation trees roots are not well developed. Whereas roots were not separated according to species, from observations, the majority of the sampled roots belonged to *Avicennia* tree. In monoplots of *Avicennia* for instance, root biomass constituted over half of the total tree biomass (53%), whereas monoplots root contribution to total biomass in *Bruguiera* and *Ceriops* was 19% and 22% respectively.

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References

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CHAPTER 5. TEMPORAL DYNAMICS OF SOIL CARBON DIOXIDE EFFLUX IN A RESTORED YOUNG MANGROVE PLANTATION AT GAZI BAY KENYA

Based on: Kirui, B., Huxham, M., Kairo, J., Skov, M. and Mencuccini, M. Temporal dynamics of soil carbon dioxide efflux in a restored young mangrove plantation at Gazi bay Kenya. (Manuscript).

CHAPTER 5. TEMPORAL DYNAMICS OF SOIL CARBON DIOXIDE EFFLUX IN A RESTORED YOUNG MANGROVE PLANTATION AT GAZI BAY KENYA

Abstract

Soil CO_2 efflux is an integrated measure of root and microbial respiration and is an important source of atmospheric CO_2. This study measured temporal variation in soil CO_2 efflux and the influence of species richness, temperature and soil moisture content in young replanted mangrove stands at Gazi bay Kenya. Soil CO_2 efflux was measured approximately every fortnight from Sept 2005 to January 2007 in thirty two plots with different mixes of mangrove species as well as controls using the soda-lime technique. Periodic measurements using an infrared gas analysis method were also carried out. Results indicate significant effects of tidal period and soil temperature on soil CO_2 efflux. Other factors, i.e., species richness, soil moisture and year did not significantly affect soil CO_2 efflux. Soil CO_2 efflux exhibited a temporal pattern which was clearly related to soil temperature pattern. Mean daily CO_2 efflux ranged from a low of 18.71 (±3.64) g m^{-2} d^{-1} to a high of 45.81 (±14.39) g m^{-2} d^{-1}. Higher soil CO_2 efflux was also found immediately after spring tides compared to the middle of neap tide. Given the observed pattern of increasing fluxes with time, we anticipate that both contributions from root respiration of planted trees as well as from microbial biomass (arising from gradual changes in sediment micro-climate caused by replanting) will increase over time.

Key words. Carbon, Mangroves, soil CO_2 efflux, soil temperature, soil moisture.

5.1 Introduction

Soil CO_2 efflux or soil respiration includes the respiration from roots and mycorrhizae (autotrophic respiration) and soil microorganisms (heterotrophic respiration) and is a major component of the forest carbon cycle (Law et al., 2002; Tüfekçioğlu and Küçük, 2004) with an annual efflux equivalent to 10 % of the atmospheric CO_2 pool (Schlesinger and Andrews, 2000). Soil CO_2 efflux is an important component of belowground carbon dynamics and storage and is altered by aspects such as substrate quality and vegetation diversity.

Measurements of soil CO_2 efflux have great potential as an indicator of ecosystem processes including metabolic activity in soil, persistence and decomposition of plant residue in soil and conversion of soil organic carbon to atmospheric CO_2 (Rochette et al., 1997; Ryan and Law, 2005). Integrated measurements can be used to estimate below-ground carbon allocation (Giardina and Ryan, 2002) and can be tied with the estimates of canopy photosynthesis to enhance our understanding of belowground carbon transfer (Ryan and Law, 2005). Frequent measurements of soil CO_2 efflux can help uncover environmental controls over decomposition (Irvine and Law, 2002) and aid with the understanding of the links between above and below-ground processes.

Temporal patterns of soil CO_2 efflux are important to models of ecosystem carbon balance (Raich and Potter, 1995). Temporal variations of soil respiration are often associated with either changes in soil temperature (e.g., Longdoz et al., 2000) or changes in both soil temperature and soil water content (e.g., Davidson et al., 1998). Few studies quantifying inter-annual variability in soil CO_2 efflux and how this is influenced by species richness have been reported (e.g., Craine et al., 2001). Inter-annual variations may result from the direct effects of environmental factors such as sediment temperature or sediment moisture, which may exhibit temporal variation (e.g., Epron et al., 2004). For instance, drought has been shown to significantly influence soil CO_2 effluxes (Davidson et al., 1998; Epron et al., 1999; Savage et al., 2001). Changes in ecosystem processes due to long term climatic variations, e.g., forest ageing or disturbances also account for variations in sediment CO_2 efflux (e.g., Coleman et al., 2002; Alongi, 2002; Epron et al., 2004).

Many comparative studies on the methods of measuring soil respiration have been conducted. However, measurement difficulties arise from inaccuracies due to the uncertainty associated with the various methods, from large spatial and temporal variability inherent in soil respiration, and from the many environmental factors involved (Norman et al., 1997). Several methods for measuring soil respiration have been employed, each with its own strengths and weaknesses. Furthermore, there is no standard or reference for determining the accuracy of any one of these methods (Nakayama, 1990). Therefore, methodological differences among investigators can become the major source of uncertainty in estimating the carbon cycle at the forest and global levels (Jensen et al., 1996). To date, the most commonly used method to measure soil respiration has been the use of static alkali absorption based upon absorption of CO_2 by alkali in solid or solution form (also referred to as the soda lime technique). This method has the advantage of integrating the efflux over time and the ability to measure many points. However, this method tends to underestimate soil respiration, especially at high rates and may overestimate soil respiration at low rates (Ewel et al., 1987; Nay et al., 1994; Haynes and Gower, 1995; Janssens and Ceulemans, 1996), and therefore global estimates of soil respiration largely based on the method may be biased. The dynamic closed chamber method (Infra red gas analysis method), which calculates soil respiration using the rates of increase of CO_2 concentration over time in a closed chamber is often regarded as a better method given that the chamber has little influence on microclimatic variables and CO_2 concentration because the measurements are made over relatively short periods (Norman et al., 1997).

Mangrove forests are a common feature in coastal zones of tropical and subtropical areas where they are thought to represent one of the major components of global C budgets (Alongi, 2002). The mangrove environment is characterized by prominent aboveground roots and peat substrates almost entirely made of fine roots (McKee, 2001, Middleton and McKee, 2001). Mangrove sediments are rich in C and Chmura et al. (2003) has reported high rates of C accumulation per unit area (mean value of 210 g C m^{-2} yr^{-1}). The high biomass allocation to aboveground - and coarse belowground roots with abundant aerenchyma ensures an adequate supply of oxygen for fine root metabolism in anaerobic sediments (McKee, 1996), whereas high C allocation to roots is thought to facilitate nutrient uptake in nutrient limited settings (McKee, 1996; 2001).

While the stocks and fixation rates of C in mangroves are well documented (Twilley et al., 1992; Twilley, 1995; Clough, 1998) and estimated to be globally significant (Ewel et al., 1998), belowground C stocks and rates of C turnover are poorly known (e.g., Ong, 1995). In July 2004, a 5-year large-scale experiment was initiated in a clear-felled mangrove area at Gazi bay in the south coast of Kenya. The experiment aims to measure how the diversity of mangrove species in replanted stands affects a range of ecosystem functions including soil CO_2 efflux. This paper presents the preliminary findings of soil CO_2 efflux measurements carried out at the established plots at the site.

The objectives of this study were;

1) To compare temporal variation in rates of CO_2 efflux in two blocks of young replanted mangrove trees and how this is influenced by tree species richness.

2) To identify the underlying environmental variables most likely causing any variations at the two blocks and among seasons within the sites and, specifically, the influence of sediment temperature, % relative soil water content and tidal influence.

5.2 Materials and Methods

5.2.1 Study Site

The study was conducted at Gazi bay, Kwale district, Kenya, 55 km south of Mombasa (4°25'S and 39°50'E). The bay has a surface area of 18 km^2, and is sheltered from strong sea waves by the presence of Chale Peninsula to the East and a fringing coral reef to the South. On the landward side, Gazi bay is bordered by 6.2 km^2 of mangrove forests. These forests are heavily used by local people as a fishing ground and a source of wood for building and fuel. As in other areas of the Kenyan coast, mangrove deforestation is widespread. The mangrove forests of Gazi have been exploited for many years especially for wood used for industrial fuel (in the calcium and brick industries in the 1970s) and building poles (Kairo, 1995; Dahdouh-Guebas et al., 2000). The clear-felling due to the industrial extraction left some areas along the coastline completely denuded.

The climate in Gazi is typical of the Kenyan coast and principally influenced by monsoon winds. Total annual precipitation varies between 1000 and 1600 mm showing a bimodal pattern of distribution. The long rains fall from April to August under the influence of the Southeast monsoon winds, while the short rains fall between October and November under the influence of the Northeast monsoon winds. It is normally hot and humid with an average annual air temperature of about 28°C with some seasonal variation. Air temperature in Gazi Bay varies between 24°C and 39°C (Bosire et al., 2003). Relative humidity is about 95% due to the close proximity to the sea.

5.2.2 Study Design

The study site was divided into two separate blocks, separated by a narrow incursion of the terrestrial zone (a grass tongue, ~15m wide). Block 1 contains sixteen plots while block two has twenty two plots all measuring 6m by 6m, and is situated on a previously deforested area. Each plot contains a differing combination of three types of mangrove species, *Avicennia marina*, *Bruguiera gymnorrhiza* and *Ceriops tagal*- A, B and C respectively, with two plots for each combination of species in each block (i.e., a total number of replicates of four per treatment). Within each plot 121 trees were planted in July 2004. The distribution of the plots within block 1 (mean height above chart datum = 3.34 m) is higher than block 2 (mean height above chart datum = 3.24 m). Block 2 also receives the tide before block 1 as it is slightly lower on the shore.

5.2.3 Measurement of CO_2 emissions

Soil CO_2 efflux rates were measured periodically immediately after the spring high tide and at the middle of neap at two random locations within each plot from September 2005 to January 2007 using the soda lime method (e.g., Edwards, 1982; Raich et al., 1990). The soda-lime method is a well-established method for the determination of soil CO_2 effluxes where a very large spatial coverage is required, or large number of treatments is present. It may underestimate actual soil CO_2 efflux rates at high efflux rates (Ewel et al., 1987) but has been also reported to overestimate flux rates when fluxes are small (Janssens and Ceulemans, 1998) the logic being that when concentrations of air chamber CO_2 are low, the soda lime scavenges it, thereby creating a diffusion gradient from the soil driving additional CO_2 up; whereas at high flux rates the logic is that there is so much CO_2 coming off the soil in the chamber that the soda lime cannot absorb it all and some diffuses away in the soil under the chamber). However the method does distinguish between higher and lower efflux rates and therefore, it is an appropriate method for comparing sites.

Plastic buckets (14.8 cm high and 20 cm in diameter) were inserted 2 cm into the sediment of young mangrove plots. Open glass jars containing approximately 30 g of soda-lime (pre-dried for 48 hrs at 80 °C before weighing) were placed at the centre of each of the buckets for a period of 24 hours with the tops of the buckets covered. After this, the jars were sealed and taken to the laboratory where the soda lime was oven-dried for 48 hrs at 80°C and weighed. Blanks were used to account for CO_2 absorption during drying and handling (Raich et al., 1990). Soda lime weight gain was multiplied by 1.69 to account for water loss (Grogan, 1998). The corrected difference in dry weight before and after the sampling represents the carbon dioxide absorbed.

Measurements carried out by the soda lime technique were periodically calibrated using a gas exchange system based on a closed dynamic approach (PP System, UK). In our experience, this double sampling scheme allowed us to obtain both a very good spatial coverage of all the experimental plots (including within-plot variability) as well as accuracy of absolute values. The PP system consisted of a soil respiration chamber (11 cm diameter) linked to the respiration EGM 2 system. The soil chambers were placed on PVC collar (thin-walled polyvinyl chloride pipe) of about 35 cm^2 area. Two collars were placed in each plot. Data were logged while the CO_2 concentration rose through the ambient level. Measurements were replicated two times in each collar and the average was taken.

5.2.4 Soil Moisture and Temperature

Soil temperature and moisture at a depth of 5 cm were measured within each chamber immediately after the soda lime jars had been collected using a single temperature sensor buried at a depth of 5 cm in the center of each chamber. Each time soil CO_2 efflux measurements were made; plot-level soil moisture was determined by taking two soil samples in each plot at 4 cm depth and drying them at 80 °C for 24 hours.

5.2.5 Statistical analysis

Differences between the parameters were tested using General Linear Model (GLM) ANCOVA after checking for normality and homogeneity of variance in the two methods. Where the above criteria were not met, data was log transformed. The model included the experimental treatment and year as fixed factors, tidal period as a dummy variable, and the individual jars as a random factor nested within the treatment. Soil temperature and % water content were also added as covariates. Regressions were used to explore the relation between CO_2 effluxes and abiotic factors (temperature and soil moisture). A significance level of $p = 0.05$ was accepted. All analyses were performed using MINITAB version 14 software.

5.3 Results

5.3.1 Temporal trends of soil CO_2 efflux

Soil CO_2 efflux exhibited a weak temporal pattern (Figure 5.1a) which reflected changes in soil temperature and soil moisture (Figure 5.1b, c). Daily average values of soil CO_2 efflux ranged from 18.71 ± 3.64 g m^{-2} d^{-1} in mid neap tide in December 2005 to 45.81 ± 14.39 g m^{-2} d^{-1} immediately after spring tide in November 2006. Higher effluxes were recorded immediately after high spring tide compared to in the middle of neap tide. Daily soil temperature ranged from a high of 35.94 ± 0.43°C in February 2006 to a low of 26.94 ± 0.43°C in April 2006. High temperatures were recorded at mid neap tide period compared to immediately after spring but overall temperatures were higher in 2005 when there were failed rains.

Soil water content did not exhibit a clear temporal pattern. However a general rising trend over time was observed, perhaps indicative of the influence from shading provided by the growing trees. Soil water content was minimal in October 2005 (8.53% ± 1.68) and was highest in June 2006 (20.63% ± 3.70) (Figure 5.1c). The low soil water contents in 2005 could also be attributed to the failed rainfalls in that year.

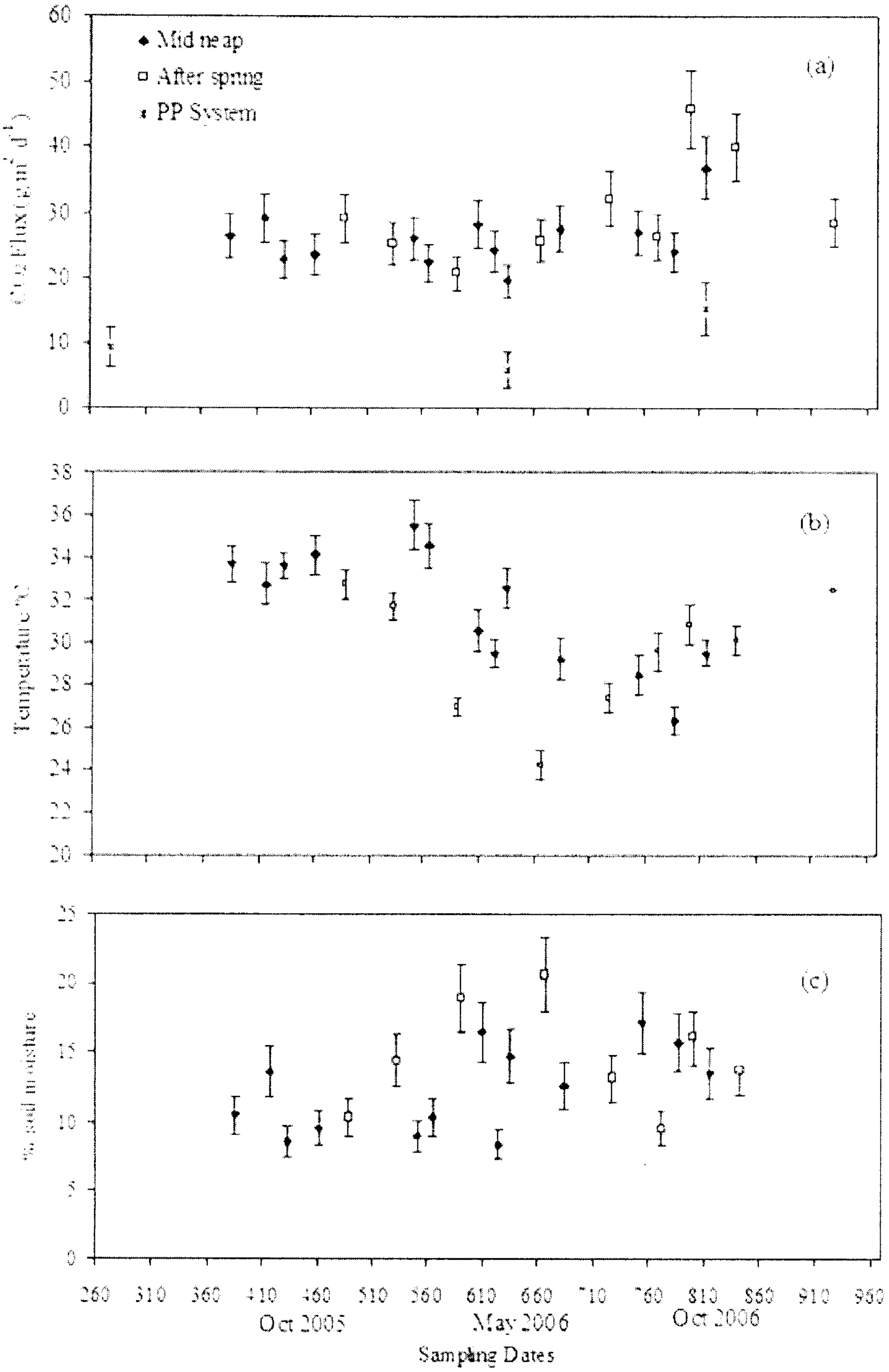

Figure 5.1 Pattern of mean (± s.e) a) CO_2 efflux using soda lime method and Infrared Gas Analysis system (PP system) b) soil temperature and c) soil moisture between the sampling periods. Sampling dates are the number of days since the trees were planted.

5.3.2 Influence of environmental variables on both methods (Soda lime and IRGA method)

A range of factors were examined for possible influence on soil CO_2 efflux, these included species richness, blocks, tidal regime, jar, and year of sampling. Soil moisture content and soil temperature were included in the analysis as covariates and the results are shown in Table 5.1 below.

Table 5.1: ANCOVA table showing effects of various factors on soil CO_2 efflux obtained using Soda lime method sort alphabetically

Source	df	ss	ms	f	P
Soil moisture	1	0.005	0.005	0.45	0.501
Temperature	1	0.075	0.075	6.65	0.010
Species richness	7	0.03923	0.00560	0.50	0.839
Tide period	1	0.61934	0.61934	54.70	<0.001
Species richness × Tideperiod	7	0.06578	0.00940	0.83	0.562
Jar No	61	0.44154	0.00724	0.64	0.986
Year	1	0.02139	0.02139	1.89	0.170
Error	1153	13.05525	0.01132		
Total	1232				

Over the sampling period, variability in soil CO_2 efflux could be attributed to soil temperature and to whether sampling was carried out immediately after spring tide (Table 5.1). On average, there was higher efflux immediately after spring tide (16 % increase) compared to at the mid neap tide (Figure 5.2). Soil temperature caused negative effects on soil CO_2 efflux (Table 5.1) although the single-variate regression was non-significant (r^2= 0.04, p= 0.36). Other variables did not have significant influence on soil CO_2 efflux. Levels of species richness did not significantly affect soil CO_2 efflux.

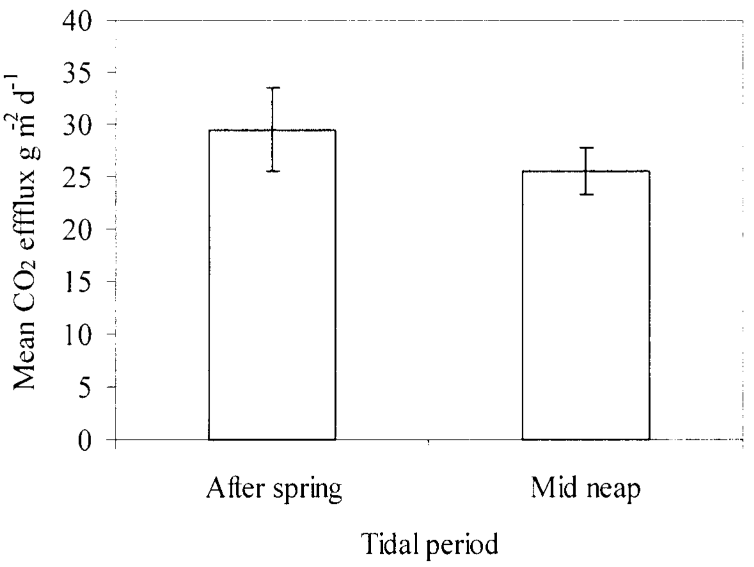

Figure 5.2: Mean ± (S.E.) Soil CO_2 efflux at spring and neap tides.

We similarly performed an ANCOVA using data obtained from the Infrared gas analysis method. This revealed some discrepancies regarding the significant environmental controls and soil moisture was the variable responsible for the observed differences in CO_2 efflux (Table 5.2). Again, species richness was not found to be a significant variable in this analysis.

Table 5.2: ANCOVA table showing effects of various factors on soil CO_2 efflux obtained using the PP-Systems method

Source	df	ss	ms	f	P
Soil moisture	1	0.052	0.052	5.93	0.021
Temperature	1	0.16	<0.001	0.03	0.858
Species richness	7	0.028	0.003	0.46	0.857
Tide period	1	0.00	0.001	0.14	0.709
Jar No	1	0.052	0.052	6.03	0.020
Error	32	0.278	0.008		
Total	43	0.559			

5.4 Discussion and Conclusion

The CO_2 efflux patterns observed over the study period appear to be linked to the patterns of soil temperature and to the tidal cycle. Previous studies have reported similar patterns in the relationships between soil CO_2 efflux and soil temperature in temperate forests (e.g., Davidson et al., 1998; Epron et al;

1999). While these have normally reported a positive relationship we surprisingly found a weak negative relationship between these two factors. We attributed this difference to variation in site characteristics. Most of the documented studies have been conducted in temperate regions where temperature values are relatively low. In our study, high temperatures were consistently prevalent. Soil CO_2 efflux is a product of two processes, i.e., heterotrophic respiration through microbial organisms and root respiration. Microbial organisms are highly sensitive to high temperatures and in our plots there was little vegetation cover due to the young age of the planted trees. We therefore envisage that higher temperatures reduced microbial activity in the sediment which consequently reduced soil CO_2 efflux. Negative relationships with soil temperatures have also been reported in studies where high soil temperatures were associated with soil drought conditions (e.g. Davidson et al., 2006; Brando et al., 2008). Similarly, our findings that the tidal cycle significantly affected soil CO_2 efflux may also be interpreted to indicate that neap tide presented settings similar to drought hence reduced CO_2 efflux.

The fluxes measured by soda lime method were higher than from the Infra-red gas analysis (IRGA method). This is in conformity with studies that have reported higher fluxes from soda lime method especially at low respiration rates (Ewel et al., 1987; Rochette et al., 1992; Jensen et al., 1996). Several reasons may explain the differences including soda lime absorption ability which is high at low concentrations hence causing differences in absorption rates and soil CO_2 diffusion (it is unlikely that production is altered); also the chamber closed for 24 hours may cause changes in temperature and soil moisture all which have effects on soil CO_2 efflux rates.

The increasing trend over time in soil CO_2 efflux observed in this study, (although not significant) could be attributed to developing root biomass. Mangroves are known to sustain a high ratio of root to shoot biomass (Chapter 4, Figure 4.4; Lovelock et al., 2006; Kairo et al., 2008), the high root biomass with aerenchyma cells providing the oxygen necessary for root metabolism. Shading effects by the young growing trees progressively modified the microclimatic conditions under these trees, perhaps leading to increases in microbial biomass.

Previous studies have reported increasing trend in soil CO_2 efflux with the age of trees, for instance Ewel et al. (1987) found that soil CO_2 efflux rates for a 29-year-old Florida slash pine plantation were 35% higher than the observed rates for a 9-year-old plantation. They attributed the higher efflux rate to the increase in live root biomass observed in the older plantation. However, although the general pattern of soil CO_2 efflux in this study showed marginal increase over time, regression analysis sowed insignificant relationship with a host of biotic variables including aboveground and root biomass values in the plots. However, given the design and the objectives of our study, which did not partition the relative contribution from roots and microbial respiration; we cannot attribute the link between stand development and increasing soil CO_2 efflux to biotic factors at this stage of stand development.

CO_2 efflux was not influenced by the species diversity in the plots. Our random sampling in the plots may have missed a systematic pattern in CO_2 efflux around the tree roots. Also, the relative young age of the stand and the subsequent low biomass in its belowground and aboveground components amongst the different species meant that there was low level metabolism. We envisage that as the trees matures the species diversity effect may become apparent, as for example in the BioCON experiment (Reich et al., 2001), where significant reduction in soil CO_2 efflux was attributed to decrease in plant diversity (Craine et al., 2001).

In this study, soil moisture did not influence soil CO_2 efflux, however the tidal period effect confounded the relative contribution by soil moisture. Due to the unique location of the mangrove in the intertidal area, periodic tides influence the soil moisture regimes at the site. Indeed in this study we found higher soil CO_2 efflux at the period immediately after spring tide compared to at mid neap tide. At neap tide the day temperatures are high from direct solar irradiation, possibly inhibiting microbial respiration, however at spring tide, the sediment is under regular rewetting and hence the sediment temperature is relatively lower. Birch (1958) reported that in drying and subsequently rewetting of soil by precipitation, there is a sudden 'burst' of decomposition, mineralization and CO_2 release and recent observations made in the Mediterranean climate of southern Europe using eddy covariance methodology have demonstrated this effect at the ecosystem level (Jarvis et al., 2005).

In conclusion, three years after planting, soil CO_2 efflux in the plots is still largely controlled by environmental factors and the influence of vegetation diversity is not detectable, largely as a consequence of the harsh environmental conditions and the slow rates of growth by the trees at the site (Kirui et al., 2008). However there was some limited evidence of increasing soil CO_2 efflux with time, suggesting an increase contribution by plant roots and perhaps from increasing microbial diversity due to changes in the sediment micro-climate. We predict influence of species richness to become apparent as trees mature.

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CHAPTER 6: SYNTHESIS CONCLUSION AND RECOMMENDATIONS

6.1 Introduction

Evidence of how human domination of ecosystems has led to massive degradation and alteration of ecosystem processes and reduced their ability to provide goods and services is now well documented (e.g. Constanza 1997; Vitousek 1997; Kareiva et al. 2007). There are several theories showing how ecosystem functions may respond to rapid species loss (reviewed in Huxham and Sumner, 2000) and experiments have provided evidence that reduced species diversity may impair ecosystem processes such as plant biomass production (Tilman et al., 1997; Hector et al., 1999). Initially, these experiments were short-term and small-scale; however, over the recent past, large-scale long-term manipulative experiments addressing issues of biodiversity and ecosystem services in terrestrial ecosystems have been established (reviewed in Scherer-Lorenzen 2005; Scherer-Lorenzen et al., 2007).

Several approaches have been adapted to assess the significance of biodiversity in forest ecosystem functions, these include comparison of existing stands of different species diversity to study a range of ecosystem functions, however with this approach, variations in environmental attributes conceals potential variations in biodiversity ecosystem process within the habitats (Hector et al., 1999). Numerous studies on mangrove land-use history have been reported and therefore have the potential to be used to document the correlations between diversity and ecosystem processes; however these cannot be used to establish causality or the underlying mechanism responsible for a relationship (Caspersen and Pacala, 2001). Hence manipulative experiments with random allocation of diversity treatments to plots while keeping environmental conditions as constant as possible are desirable (Scherer-Lorenzen et al., 2005). These approaches have been reported in grasslands (Loreau et al., 2002) aquatic microcosm (Kinzig et al., 2002) and more recently in the terrestrial forests (see review in Scherer et al., 2005). To my knowledge, these are the first findings from a manipulative biodiversity-ecosystem function experiment conducted in a mangrove ecosystem. While the findings are not in themselves conclusive given the short period of the project. They nevertheless provide some early perspective on the extent of species richness effects on a range of ecosystem functions from this highly dynamic intertidal system.

6.1.1 Selection and Complementarity Effects

It is clear now that there is a link between biodiversity and ecosystem function given the number of experiments that have documented this link (reviewed in Wardle, 1999; Schwartz et al., 2000; Loreau et al., 2001, 2002; Hector, 2002; Schmid, 2002; Hooper et al., 2005; Spehn et al., 2005). However, the mechanisms causing this relationship are still debatable. Two schools of thought have emerged: the 'sampling effect' hypothesis which suggests that diversity effects are caused by the greater chance of one or few dominant, high biomass species being in the mix and the 'niche complementarity effect' hypothesis which states that differences in niches between species should lead to efficient resource utilization and consequent high productivity (Huston, 1997; Tilman et al., 1997, 2001). Thus, each hypothesis proposes an ecologically distinct mechanism, complementarity involving interactions among two or more species and sampling involving the presence of a particular species. However, these two effects are not mutually exclusive rather overlaps between the two can occur over large time spans (Fargione et al., 2007).

This study has shown no effects of species richness on sapling survival, soil CO_2 efflux. A combination of factors may be responsible including, young age of the plantation and strong environmental influence. However there were significant species richness effects particularly on growth parameters. Meta-analysis and results from long term (10 years) monitoring of grassland experiments have shown species richness effects with selection effects being responsible for biodiversity effects in the short-tern and species complimentary being responsible over long periods (Tilman et al., 2006; Fargione et al., 2007; Cardinale et al., 2007). The current work concurs with these studies in finding a strong selection effect in the early stages of growth but it is envisaged that complementarity may emerge more strongly in the current work in subsequent years. For instance the recruitment of wildlings and the shading traits by *Bruguiera* may reduce surface evaporation subsequently ameliorating environmental conditions particularly salts in the mixed plots which may help less tolerant species.

Experiments looking at species richness effects on a range of responses should, as much as maximizing species richness, ensure that the species selected should have tolerance to environmental conditions prevailing at site. Much as the advice has been to site experiments in areas with homogeneous environmental conditions, experience show that attaining environmental homogeneity is difficult even within local scales

6.1.2 Mangrove Sapling Survival

Mangrove reforestation initiatives are often held back by high sapling mortalities especially during the early critical stages when saplings are adjusting to changes in environmental settings (Lewis, 2005). Several abiotic and biotic factors are known to influence sapling establishment and growth and include: tidal regime (Rabinowitz, 1978), soil characteristics (Mckee, 1995), sapling dispersal mechanism (Minchinton, 2006), propagule provenance (Kairo et al., 2001) and predation of propagules (Robertson et al., 1990). Most mangrove production forestry as practiced in South East Asia (e.g. 1928; Putz and Chan, 1986) has tended to concentrate on monoculture of the dominant species leading to loss of productivity (see e.g. Ong, 1995).

Effects of species diversity, sapling structural attributes and environmental variables on sapling survival were assessed at two sites replanted with mangroves. Neither sapling size nor position influenced species survival (Kirui et al., 2008, Chapter 2: Figure 2.2 & Table 2.3). Thus large sapling size at the time of planting does not result in greater survival; hence restoration efforts do not need to increase size (and therefore expense) before planting. At site 1, 416 days after planting, there were large differences in mean survival rates between the three species planted at the different plots in the site. *Avicennia marina* had the highest survival (87 %) and *Bruguiera gymnorrhiza* had the lowest survival rate (29 %). However the survival rates were not influenced by species mix. Of the environmental variables sampled, sediment salinity exerted the strongest effect on sapling survival (Chapter 2, Figure 2.2 and Table 2.2). *Bruguiera gymnorrhiza* in particular suffered high sapling losses which were linked to salinity levels thus suggesting that this species was not well suited to the conditions that were prevalent at the site, which was surprising in that one of the premises on which we based including this species as one of the saplings to be planted was the fact that before clearance it was a species found at this site and was also present in adjacent mangrove woods. There were no species richness treatment effects on sapling survival and on a suite of environmental variables.

Success of restoration programs in clear-felled lands left exposed for long periods largely hinges on planting species with tolerance traits to environmental factors specific to the location. Ideally, identification of species that grow naturally in the vicinity of a proposed restoration site should be an important criterion in deciding the species to plant in a restoration site. However, it is evident that low survival in some species - for instance in this study (Chapter 2) - that this may not always work out due to several reasons including; sites may undergo hydrologic and other physical changes after being cleared (Field et al., 1998); patterns of distribution among the mature trees may not be represent early growth traits, (Clarke et al., 2001) and finally there may be variations in environmental conditions even at small scales. Therefore the best approach to successful mangrove restoration may involve measurement - even at a small scale - of baseline environmental factors with the potential to influence early tree growth.

6.1.3 Natural Recruitment

Initial stages of growth by saplings are critical to survival and subsequent development into adult trees, in the process determining the structure of a stand (Bosire, 2006). Several factors combine to shape the development of saplings into mature trees. These include sediment conditions, hydrology, and herbivory (Yong et al., 2005). An important ecosystem function performed by restored plantations is the recruitment of wild trees into the stand improving the stand structure, composition and thereby species diversity. However, few studies have been conducted on this ecosystem function in mangroves; those that have were based on mono-plantations (e.g. Bosire et al., 2003) and the influence of species diversity on this ecosystem function has hardly been reported.

A facilitation effect was observed in the recruitment of wild plants with *Avicennia marina* acting as a 'nursery species' for recruits of other species, particularly *Ceriops tagal*. Bosire et al. (2003) working on a reforested mono-plantation of

R. mucronata observed significant recruitment of non-planted trees which subsequently contributed to increased stand structure and development. We found a significant treatment effect on wildling recruitment and a 'nursing effect' with high recruitment and survival observed in plots containing *Avicennia* among the mix of planted species.

Two mechanisms are probably responsible for the observation; first, the broad shallow network of *Avicennia marina* pneumatophores may have facilitated propagule settlement by physically trapping propagules. Bosire et al. (2003) observed no colonization in a bare *S. alba* stand in comparison with reforested and naturally growing mangrove stands. He attributed this to daily exposure to inundation which exposed the propagules to wave action and tidal currents. Second, given the superior growth and survival characteristics of *Avicennia* at this site, the trapped propagules may have benefited from the impacts of *Avicennia* on the microhabitat within the plots, in particular greater shading and increased sediment moisture and carbon accumulation. The operation of both of these mechanisms was evidenced by the higher numbers of wildings and their better rates of survival in the plots including *Avicennia*.

These findings illustrate the different interspecific roles played by mangroves in facilitating recruitment of non-planted species into the stands, in fact the facilitative effects of replanted trees has been shown to affect not only the tree wildling recruitment but has been shown to influence the recruitment of other taxonomic units i.e. crabs in our study site (Skov et al., in prep). However, it is clear that successful recolonization by wild species will not only depend on structural and functional traits of the planted trees but will also be influenced by environmental settings including flooding regimes and salinity levels.

6.1.4 Biomass Production and Partitioning

Harsh environmental conditions meant slow growth coupled with high mortality in one of the species planted during the first two years (Chapter 2) and consequently biomass values during this period were low. However by 2007 there were significant treatment effects on a range of growth parameters including aboveground biomass, mean tree height, leaf area index and wildlings recruitment. *Avicennia marina* showed strong competitive traits; with the best growth overall and enhanced growth of individual trees when planted in mixed species plots. Initial plot height above sea level showed positive relationships with plot biomass, whilst sediment salinity, ammonia and phosphate concentration showed negative relationships.

Total biomass production was generally higher in *Avicennia marina* than in the other two species (*Bruguiera gymnorrhiza* and *Ceriops tagal*). This variation may be explained by the differences in tolerance to hypersalinity levels discussed previously (Chapters 1, 2 and 3). Plots with *Avicennia* in their mixtures recorded higher biomass values compared to those without (Chapter 3). *Avicennia* has tolerance to a wide variety of environmental conditions and is regarded as a pioneer species colonizing a site and subsequently changing the sediment conditions to favour other species. Removal of the initial forest cover at the field site had led to salinisation of the sediment and a total lack of natural regeneration; under these conditions, it was necessary to plant nursery-reared trees to initiate restoration, and our results suggest *Avicennia* acts as a 'superplant' (Zedler et al., 2001) in fostering ecosystem recovery.

High allocation of biomass to belowground components by mangroves has been reported in a number of studies e.g. in Belize and Australia (Mckee and Faulkner, 2000; Snowdon et al., 2000). Other reports have emphasized the importance of environmental stressors e.g. salinity, hydroperiods as well as resource limitations in determining biomass allocation to roots. In this study, biomass allocation either to the aboveground components or the belowground parts was highly influenced by the presence of *Avicennia*. The root shoot ratio observed in the *Avicennia* compares well with *A. marina* root: shoot ratios observed in Australia (Briggs, 1977; Saintilan, 1997b) although is higher than that reported by Mackey (1993) also in Australia (Table 6.1). Interestingly, Saintilan (1997a) reported root: shoot ratio of 4.1 in Australia in a hyper-saline soils. He further observed low root shoot ratios in areas where salinity did not exceed the sea water levels and higher root shoot ratios in areas where salinity was high thus suggesting that *Avicennia* responds to hypersalinity by allocating more biomass to belowground components.

Table 6.1: Root: shoot ratios for mangrove forests from different studies around the world.

Species	Location	Source	Root:shoot
A. marina	Australia	Briggs, 1977	1.02-1.41
A. marina	Queensland	Mackey, 1993	0.58
A. marina	Queensland	Saintilan, 1997b	0.4-3.1
A. marina	Northern Australia	Comley and McGuiness, 2005	
A. marina	This study		1.2
B.gymnorrhiza	Japan	Komiyama et al., 1989	1.39
B. gymnorrhiza	This study		0.3
C. tagal	Australia	Matsui, 1998	0.42
C. tagal	Thailand	Komiyama et al., 1987	0.96
C. tagal	This study		0.3

Root production, biomass and root: shoot ratio values in this study were generally low and showed variation with species. This indicates that three years after plantation tree roots are not well developed. Roots from mixed plots were not separated according to species in this study; however from observation, the majority of the sampled roots belonged to *Avicennia*, for instance in monoplots of *Avicennia*, root biomass constituted over half of the total tree biomass (53%), whereas root contributions to total biomass in *Bruguiera* and *Ceriops* monoplots were 19% and 22% respectively. It should be noted that different species have different growth traits. For instance, *Avicennia* has extensive underground cable roots system whereas other species like *Bruguiera* lack woody roots belowground (Gill and Tomlinson, 1977). Also difficulties in obtaining root biomass studies on this aspect are few (but see Table 6.1 above) and the methods highly variable hence making comparisons of the studies difficult.

6.1.5 Environmental Context

There have been many inconsistencies reported in the form and the cause of the relationship between species diversity and ecosystem function. For instance, a review by Johnson et al. (1996) emphasized the variation among empirical studies that have found contrasting relationship between the species numbers in a system and primary productivity – an ecosystem function of widespread interest. Even where studies agreed on the direction of the diversity-productivity relationship, there was considerable variation in the magnitude of change in productivity over levels of species diversity. The controversies regarding these inconsistencies have given rise to the third dimension of the contribution of the environmental context and it has been argued that there may never be a single generalizable relationship between species richness and ecosystem functioning given that the contribution of species diversity and compositions to ecosystem processes are dependent on the environmental context (Cardinale et al., 2000). In fact several studies have reported strong effects of environmental context over species richness (e.g. Villa et al., 2003).

Salt tolerance varies widely between species. For instance while *A. marina* does not survive well in non-saline soils (Downton, 1982, Clough, 1984), other mangroves e.g. *Bruguiera gymnorrhiza* and *Ceriops tagal* grow well in medium-saline soils (Clough, 1992). Salinity stress poses the problem of the need to use energy to maintain osmotic balance thereby expending energy that might otherwise be used for growth and primary productivity (Clough, 1992). Table 2.2 in Chapter 2 and Table 3.3 in Chapter 3 show multiple regressions of effects of initial environmental conditions on aboveground biomass and belowground biomass respectively. Salinity exerted the greatest negative influence on biomass productivity (both above and below ground) as well as sapling survival, followed by ammonia. Boto et al. (1985) reports that prolonged exposure to ammonium ions in the absence of nitrates led to marked reduction in growth and eventual death of *Avicennia marina* seedling.

Hydrology exert controls over an array of ecosystem functions including biomass production and is responsible for the variation in mangrove productivity among mangrove types, species, or stage of development, e.g., high values in riverine forests to low values in scrub forests (Twilley et al. 1986, Day et al. 1996). Variation in tolerance to flooding regimes is common among species. For instance, while *A. marina* has a wide tidal gradient, more so due to its wide salinity tolerance, other species like *B. gymnorrhiza* and *C. tagal* are mostly found in the high and medium tidal levels (Clough, 1992). While the plots were within a narrow tidal height above datum, surprisingly, there was significant plot height effect on growth parameters (Chapter 3 & Chapter 4). There was low colinearity between salinity and the plot heights hence suggesting other mechanism to be responsible for the observed variations. In summary whereas there may be the need to optimize species richness in attempting to maximize biodiversity, this findings advocate for the need to focus on species that match environmental context.

6.1.6 Carbon Dioxide Efflux

The rise in global atmospheric carbon dioxide concentrations has led to increased atmospheric temperature triggering a series of shifts in biogeochemical functions. High temperatures stimulate higher photosynthetic activities leading to accelerated accumulation of carbon in forest systems. However, higher temperatures also lead to increased mineralization rate of organic carbon pools in soils by heterotrophic organisms thus countering the forest 'carbon sink' attributes. Annual soil carbon flux in young mixed replanted mangrove stands in Gazi bay Kenya was quantified using the soda lime technique and compared to periodic findings obtained using Infra red gas analyser (PP system). Results showed tidal period (whether spring or neap tide) and sediment temperature effects on soil CO_2 efflux. Soda lime technique had consistently higher soil CO_2 efflux values compared to those obtained from the infra red gas analyser. Mean soil efflux ranged between 18.71 (± 3.64 g m^{-2} d^{-1})

and 45.81 (± 14.39 g m^{-2} d^{-1}). Previous studies have shown that the soda lime technique overestimates soil CO_2 efflux values at low concentrations, perhaps suggestive in this case that our plots had lower carbon dioxide concentrations. Given the slow growth of the saplings at the plot and the short time the study ran, species richness effects were not apparent in this study suggesting that the low fluxes observed were probably from the microbial activities.

6.2 Conclusion and Recommendations

In conclusion, this work suggests the following for mangrove restoration attempts at degraded sites such as the one studied here:

1. Use species with the highest tolerance traits for the environmental conditions at the restoration site. This is particularly more so in degraded areas that have been left bare for long periods because exposure leads to changes in sediment physico-chemical conditions

2. While it is important to use nursery-reared species during planting, the size of the saplings and by extension -age at planting- does not appear to be important during transplanting process, consequently there is no advantage in having seedlings kept much longer in the nurseries before transplanting

3. In mixed species replantation projects species selection effects become apparent in the early development years of the tree growth but other concurrent

stand structural development e.g. Shading effects from tree species with high leaf formation; may lead to gradual shift to dominance by species complementarity effects.

4. There is variation in the period at which various ecosystem processes become apparent, for instance while difference in biomass allocation manifest early enough (three years in this study) it is apparent that other process e.g. soil CO_2 efflux may take much longer.

And the following recommendations for future work on biodiversity ecosystems functions in mangroves are put forward;

1. Experimental evidence that plant species diversity has positive effects on biomass production appears to conflict with correlations of species diversity and standing biomass in natural communities. This may be due to the confounding effects of a third variable, resource availability (specifically nutrients), which may have strong control over both diversity and productivity in natural systems and may conceal any positive effects of diversity on productivity. To test this hypothesis there is therefore a need to conduct simultaneous experiments where the effects of resource availability and species richness on productivity are tested.
2. We do not fully understand the consequences of removal of large volumes of timber from the mangrove forests on sediment characteristics. Ewel

et al, (1998) postulates that sediment compaction arising from over-extraction of timber could lead to lowered redox values as the roots decompose. It is important to quantify effects of lowered redox on sediment geochemistry, for example this could lead to increased release of N_2, H_2S and perhaps CH_4 to the atmosphere. We thus need to understand these dynamics in mangrove processes and functions which could be useful in formulating local, national and regional mangrove management plans.

3. Shifts in mangrove structure and distribution triggered by climate change have been predicted (McKee et al., 2007). What is not known is how these shifts will impinge on the nature of plant- plant interaction. For instance, Elsol and Saenger (1983) have found that the distributions of *Ceriops tagal* and *Avicennia marina* overlapped to a large extend and that their relative importance varied depending on the environmental conditions. There is therefore need to understand how the three species used in this study interact at varying environmental conditions.

4. In this study, we did not observe edge effects on tree survival, possibly due to the small sizes of our plots, however there is evidence that edge effects could be appearing as the trees grow, for instance there is a noteworthy difference in heights between trees at the edge and those in the middle of the plot. Other aspects that need to be understood include the effects of distance between trees.

5. Soil CO_2 efflux is a product of two processes; root respiration and microbial organism respiration. This study measured total soil CO_2 efflux as it was not possible to apportion the fluxes observed to any of the two respiration sources. There is therefore need to further follow up on the partitioning the relative contributions. This has been successfully conducted in terrestrial systems (see review in Kuzyakov, 2006).

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