THE IMPACTS OF TREE DENSITY ON THE PHYSICAL AND BIOLOGICAL CHARACTERISTICS OF PLANTED MANGROVE STANDS IN SRI LANKA

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Authorship Declaration

I, **Marappullige Priyantha Kumara,** declare that the work undertaken for this PhD dissertation has been undertaken by myself and the final dissertation produced by me. The work has not been submitted in part or in whole in regard to any other academic qualification.

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ABSTRACT

Survival, growth, aboveground biomass production, belowground biomass production, sediment accretion, soil surface elevation dynamics, sediment carbon and C/N ratio, sediment N and P, sediment ^{13}C and ^{15}N, sediment texture and macrofauna community structure, were studied in experimental treatments planted with four different densities (6.96, 3.26, 1.93 and 0.95 seedlings m^{-2}) of the mangrove *Rhizophora mucronata* in Palakuda, Puttalam Lagoon, Sri Lanka. The first three parameters were also studied at a replicated experiment at Rekawa Lagoon, Sri Lanka. For both Palakuda (1,171days) and Rekawa (702 days) sites, the highest tree density (6.96 seedlings m^{-2}) showed significantly higher % survival: means (±S.E.) of 93.4 (± 1.1) and 91.2 (± 1.38) respectively. The measures of individual trees (tree height, stem diameter, number of leaves, leaf area, number of branches, number of prop roots) did not differ among treatments ($p>0.05$) for both sites. In contrast, the aboveground biomass responded significantly to planting density with higher plantation densities equating to greater biomass: 10772 ± 24 and 9904 ± 18.1g dry weight m^{-2} for Palakuda (1,171days) and Rekawa (702 days) respectively. The belowground biomass at Palakuda (1370 days) varied significantly between the densities with the highest belowground biomass (105.41 ± 6.98 g m^{-2}) in the highest tree density. The same tree density had the highest numbers of fine roots m^{-2} for efficient absorption of nutrients. Higher tree densities accumulated more N in their sediments while the sediment phosphate was not different between the densities. Sediment ‰ $\delta^{13}C$, ‰ $\delta^{15}N$ and C/N ratios ranged between -16.41 to -14.58, 2.80 to 2.40 and 9.32 to 7.85 respectively and were independent of the planting density. The δ^{13}C values indicated a potential mix of seagrass C and mangrove C in sediments of the treatments; the highest tree density (6.96 seedlings m^{-2}) had significantly higher % sediment carbon (0.68 ± 0.04) compared with the unplanted controls (0.46 ± 0.05). Rates of surface accretion were 13.0 (± 1.3), 10.5 (± 0.9), 8.4 (± 0.3), 6.9 (± 0.5) and 5.7 (± 0.3) mm year^{-1} at planting densities of 6.96, 3.26, 1.93, 0.95, and 0 (unplanted control) seedlings m^{-2} respectively, showing highly significant differences among treatments. Mean (± SE) rates of surface elevation change were much lower than rates of accretion at 2.8 (± 0.2), 1.6 (± 0.1), 1.1(± 0.2), 0.6 (± 0.2) and -0.3 (± 0.1) mm year^{-1} for 6.96, 3.26, 1.93, 0.95, and 0 seedlings m^{-2}, respectively. The community structure of the sediment macrofauna was unchanged between the treatments; that is likely to be the result of unchanged sediment texture and unavailability of mangrove derived carbon as the major food source. This study demonstrated the role of higher mangrove densities in enhancing the rates of sediment accretion and surface elevation processes that may be crucial in mangrove ecosystems' adaptation to sea-level rise. There was no evidence that increasing plant density evoked a trade-off with growth and survival of the planted trees during their early 1171 days of growth. While these potential processes need further research, the enhanced survival at high densities suggests the potential to use high plantation densities to help mitigate sea-level rise effects by encouraging positive sediment surface elevation. Higher biomass production in higher densities would also help faster sequestration of atmospheric carbon dioxide.

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Table of Contents

CHAPTER 1-GENERAL INTRODUCTION

CHAPTER 2-THE EFFECTS OF DENSITY ON SEDIMENT ACCRETION AND SOIL ELEVATION IN MANGROVES

CHAPTER 3- EFFECTS OF DENSITY ON GROWTH AND BIOMASS PRODUCTION IN PLANTED MANGROVES

CHAPTER 4-EFFECTS OF THE TREE DENSITY ON SEDIMENT MACROFAUNA IN PLANTED MANGROVES

CHAPTER 5- SEDIMENT CARBON SOURCES AND TEXTURE AMONG DIFFERENT MANGROVE DENSITIES

CHAPTER 6- SUMMARY AND CONCLUSIONS

List of Figures

List of Tables

List of Publications

During the course of this PhD study, the following articles were published

1) Kumara, M.P., Huxham, M. & Krauss, K. 2008. The effects of density on sediment accretion and soil elevation in mangroves (Abstract). The 29th Annual Meeting of The Society of Wetland Scientists, Washington (DC).

2) Huxham, M., Kumara, M.P., Jayatissa, L.P., Krauss, K., Kairo, J., Langat, J., Mencuccini, M., Skov, M. & Kirui, B. 2010. Intra and inter-specific facilitation in mangroves may increase resilience to climate change threats. Journal of Philosophical Transactions of the Royal Society B. 365: 2127-2135

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

4) Kumara, M.P., Jayatissa, L.P., Krauss, K.W., Phillips, D.H. & Huxham, M. 2010. High density mangrove plantation enhances the mangrove self-defence mechanisms in coastal areas susceptible for sea-level rise (Abstract). The National Conference on Identification of Knowledge Gaps for Sustainable Management of Mangrove Ecosystems in Sri Lanka. Matara, Sri Lanka.

CHAPTER I - GENERAL INTRODUCTION

This chapter will provide a basic description of mangrove biology, of the economical and ecological importance of mangroves and of current threats to mangrove conservation. The mitigation of coastal erosion through the absorption of wave energy by mangrove forests, soil building processes associated with mangrove aerial structures and the effects of mangrove floral density on tree growth, macrofauna and sediment carbon will also be reviewed.

1.1 Introduction to Mangroves

1.1.1 What are mangroves?

Mangroves are characterised by highly adapted salt-tolerant plant communities that grow at the estuaries, lagoons and sheltered sea coasts of tropical and subtropical regions (Das, 2001; Vannucci, 2001; Eslami-Andargoli *et al.*, 2009; Rajkaran and Adams, 2010). The word `mangro` was formerly the ordinary name for *Rhizophora mangle* in Surinam (Chapman, 1976), and Macnae (1968) introduced the word `mangroves` to name the plant species and `mangal` for the mangrove forest community (Das, 2001). Mangroves are considered to have originated after the first angiosperms, around 114 million years ago (Duke, 1992) and 3 major types of mangrove settings have been reported (Cintron and Novelli, 1984) according to their relative position to the water body:

1) Riverine forest type (R-type mangal) - Found on flood plains along tidal rivers, and inundated by most high tides.

2) Fringe forest type (F-type mangal) - Directly exposed to the open sea, and thus affected by sea waves.

3) Basin forest type (B-type mangal) - This forest is a partially impounded depression, and is inundated by tides.

The atmospheric temperature and moisture content strongly affect the distribution of mangroves (Duke, 1992; Saenger and Snedaker, 1993) thus they show a tropical dominance (Alongi, 2002). Mangroves are generally confined to latitudes between 30° north and 30° south; having a northern limit in Japan (31°22'N) and Bermuda (32°20'N); while the southern extensions are in New Zealand (38°03'S), Australia (38°45'S) and on the east coast of South Africa (32°59'S) (Spalding, 1997; Yang *et al.*, 1997). Thus, the global distribution of mangroves has been strongly limited by temperature while the area and the biomass of mangroves are regionally controlled by rainfall, tides and river flow (Alongi, 2002).

Mangroves are distributed in 112 countries and territories (Kathiresan and Bingham, 2001) and the estimates of global mangrove coverage range between 10 to 24 million hectares (Saenger *et al.*, 1983; Bunt, 1992; Schwamborn and Saint-Paul, 1996; Twilley *et al.*, 1992; Spalding, 1997; Valiela *et al.*, 2001). The length of time mangrove propagules remain viable, their distribution success, growth rate and the tolerance limits are species-specific and quite consistent around the world thus producing characteristic distributional ranges for most species (Duke *et al.*, 1998).

Tomlinson (1986) described a total of 54 world mangrove species in 20 genera and 16 families. Duke (1992) identified 69 mangrove species belonging to 26 genera and 20 families. By integrating Tomlinson (1986) and Duke (1992), Kathiresan and Bingham (2001) listed a total of 65 mangrove species in 22 genera and 16 families.

1.1.2 Adaptations of Mangroves

Mangroves are tidal forests having highly developed morphological and physiological adaptations to extreme intertidal conditions of high salinity, muddy and anaerobic soils, extreme tides, strong winds and high temperatures (Kathiresan and Bingham, 2001; Alongi, 2002). These adaptations include aerial roots that enable the main root system to breathe the atmospheric air, supportive roots that act against wind force and boggy soil, mechanisms to cope with high salt, viviparous embryos that avoid seed germination difficulties, and adaptations of seeds to disperse by the tide (Alongi, 2002). These adaptations differ among taxa and with the habitat physico-chemistry (Duke, 1992).

The roots of many mangrove species do not penetrate far in to the mud. Some species (*Rhizophora* sp) have special supportive roots that grow from the main stem and the branches and these lateral roots anchor the trees in to the loose mud supporting the tree (Kathiresan and Bingham 2001; Augustinus, 2004).

As the water logged soil limits root respiration, the shallow roots often send up extensions called pneumatophores to the surface. The lenticels (loosely aggregated air breathing cells) located on exposed areas of these roots facilitate exchange of respiratory air and these lenticels may be closed or opened according to the environmental conditions (Tomlinson, 1986; Nybakken, 2001).

Although mangroves are physiologically tolerant of high salt and have special mechanisms (e.g.: ultra-filters that exclude salts while extracting water from the soil) for absorbing freshwater against the strong soil osmotic pressure, they nevertheless absorb some salt during nutrient and water absorption. The transpirational streams transport these salts to leaf tissues where they must be managed before being toxic (Dschida *et al.*, 1992; Ball, 1996; Zheng *et al.*, 1999). The *Avicennia* sp., *Acanthus* sp., and *Aegiceras* sp. excrete these excess salts through specialized salt glands in their leaves (Dschida *et al.*, 1992) while *Lumnitzera* sp. and *Excoecaria* sp accumulate salts in leaf vacuoles and become succulent (Tomlinson, 1986). Two other strategies used by some mangrove species are transferring the salt in to senescent leaves or storing it in the bark or the wood (Tomlinson, 1986). Shedding of old leaves may also be used as an additional mechanism for salt elimination (Teas, 1979).

Mangrove vivipary, the continuous growth of offspring while still attached to the maternal plant, is an exclusive adaptation to shallow marine habitats (Rabinowitz, 1978; Thomas and Paul, 1996). Depending on whether or not the seedling sprouts inside or out of the pericarp, vivipary is divided into two types: cryptovivipary and exposed vivipary (Lin, 1988). The seedlings of species such as *Kandelia candel*, *Bruguiera gymnorrhiza*, *B. sexangula* and most of the Rhizophoracea members sprout out of pericarps after the seeds germinate, showing exposed vivipary (Lin, 1988; Zheng *et al.*, 1999). The seed germinates within the fruit while still attached to the mother tree, forming a spindle-like viviparous seedling termed a hypocotyle. After maturation, the seedling drops off and floats in water until it is anchored in to the mud. The roots sprout and penetrate in to the mud establishing the seedling (Lin, 1988) afterwards. The seeds of *Aegiceras corniculatum* and *Avicennia marina* remain inside the pericarp after germinating, which is termed cryptovivipary (Zheng *et al.*, 1999). The distribution of propagules depends on their buoyancy, longevity and the activity of tides and the currents (Nybakken, 2001).

1.1.3 Importance of Mangroves

The high litter degradation rates and efficient recycling of nutrients, supplied by both autochthonous and allochthonous inputs from natural and anthropogenic sources, have resulted in average productivity of 2500 mg C m^{-2} d^{-1} in mangroves making them important components of coastal biogeochemical cycles (Bouillon *et al.*, 2002). The fresh detritus from primary production enters the system and is physically, chemically and biologically decomposed making the subsequent organic materials more nutritious by microbial enrichment processes. The nutrients generated by remineralisation are ultimately made available for primary production and this in turn supports a wide variety of consumers (Odum and Heald, 1975). The muddy or sandy sediments of mangroves create unique ecological environments for a variety of epibenthic, infaunal, and meiofaunal invertebrates while the water channels within the mangroves support phytoplankton, zooplankton and fish (Kathiresan and Bingham, 2001). The muddy bottom and associated submerged roots, trunks and branches of mangroves provide habitats for various groups of fauna including Nematodes (Alongi, 1987; Hodda, 1990; Gourbault and Vincx, 1994; Verschelde *et al.*, 1995; Tolhurst *et al.*, 2010), Sponges and Ascidians (Goodbody, 1993; Bingham and Young, 1991; Rützler, 1995; Hunting *et al.*, 2009), Barnacles (Foster, 1982; Anderson *et al.*, 1988; Bayliss, 1993; Ross and Underwood, 1997), Isopods (Ellison and Farnsworth ,1990;

Santhakumari, 1991; Dahanayaka and Vijayarathne, 2009) crabs (Gherardi *et al.*,1991; Skilleter and Warren, 2000; Schories *et al.*, 2003; Priyadarshani *et al.*, 2008), Mollusks (Cook and Kenyon, 1993 ; Skilleter, 1996, Tack *et al.*, 1992; Ruwa and Polk, 1994; Lee and Williams, 2002). Polychaetes (Londoño-Mesa *et al.*, 2002; Bosire *et al.*, 2004; Metcalfe and Glasby, 2008) and Oligochaetes (Erséus, 2002; Netto and Gallucci, 2003).

Various groups of reptiles, amphibians, insects, birds and mammals also live in different mangrove sub-habitats (Kathiresan and Bingham, 2001; Alongi, 2002). Mangroves provide habitat for some threatened species such as the rare proboscis monkey, scarlet ibis, straight-billed woodcreeper, Bengal tiger (Saenger *et al.*, 1983; Loucks *et al.*, 2010), several species of yellow warblers, mangrove vireo and mangrove cuckoo that are nearly confined to mangroves (Kathiresan and Bingham, 2001; Alongi, 2002). The structural complexity resulting from submerged networks of stems and aerial roots minimize the incidence of predation meaning that mangroves are important nursery habitats for juvenile fish (Weinstein and Brooks, 1983; Robertson and Duke, 1987; Little *et al.*, 1988; Chong *et al.*, 1990; Alongi, 2002; Mumby *et al.*, 2004). Juveniles of many fish species prefer mangrove habitats over the adjacent mudflats and sea-grass bed habitats (Morton, 1990; Robertson and Duke, 1990). Mangrove organic matter inputs are important for sessile invertebrates of adjacent coral reefs (Granek *et al.*, 2009).

Mangroves can dissipate the energy of the incoming waves through their dense network of aboveground roots and stems as the increased bed roughness reduces the height of the wave (Quartel *et al.*, 2007). The wave energy decay model applied in this study also revealed that the wave height reduction caused by the resistance (drag force) of the mangroves depends on the species of the vegetation. The unique configuration of stems, prop roots and pneumatophores of the different mangrove species exerts different drag forces resulting in different reduction rates of waves (Wolanski *et al.*, 1999). Mangroves that have large pneumatophores (e.g. *Sonneratia* sp.) exert a higher drag force for incoming waves than the species (such as *Kandelia candel*) with no large pneumatophores (Furukawa and Wolanski, 1996). The wave height reduction also increases with an increase in density and height of the mangrove vegetation (Mazda *et al*., 1997; Quartel *et al*., 2007).

Evidence for coastal erosion resulting from the removal of mangroves in Thailand was documented by Thampanya *et al*. (2006) using a remote sensing study of the past 30 years. They concluded that mangrove dominated coasts exhibit less erosion while non-mangrove coasts of former mangrove areas suffered substantial erosion. This study further noted that in areas where erosion prevailed, the presence of mangroves had reduced the rates of erosion. Large scale coastal erosion experienced in southern Vietnam since the early 20th century has also been identified as a result of human-mediated transition of mangrove forests to settlements, rice cultivations, salt pans and aquaculture ponds (Mazda *et al*., 2002).

The mangrove vegetation traps suspended sediment by its complex above-ground structures, thus potentially functioning as coastal land builders (Woodroffe, 1992; Wolanski *et al.*, 1992; Wolanski, 1994; Furukawa *et al.*, 1997). Suspended sediments from various sources (river discharge, dredged material and re-suspension of bottom sediment) are carried in to mangroves with the high water and they settle in mangroves as the water movements become slow among the complex aboveground structures in the mangrove forest (Furukawa *et al.*, 1997; Kathiresan, 2003). The peat derived from their root biomass also contributes during new soil building (McKee *et al.*, 2007).

Marine and terrestrial flora synthesize organic carbon with distinct ^{13}C / ^{12}C values (Schweizer *et al.*, 1999; Smith and Epstein, 1971) which is transported in to mangroves with river discharge, tides and waves (Wolanski, 1994; Ayukai and Wolanski, 1997). Different hydrodynamic conditions (different degrees of wave attenuation and water slowing) would be required for settling of carbon from different sources and dissimilar drag forces inside different mangrove densities would provide these requirements. Mangrove carbon can be traced through isotope techniques (Fry, 2006; Bouillon *et al*., 2007; Prasad and Ramanadan, 2009; Otero *et al*., 2000; Cloern *et al*., 2002; Bauer *et al*., 2002) and isotope coupled with C/N ratios, can provide more effective indicators for identifying coastal sediment sources (Yu *et al*., 2010). Understanding the settling of carbon into mangroves having different morphology (including different densities, positions on the shore and different species) would help in manipulating mangrove plantations for trapping and sinking the carbon suspended within coastal water.

Economically, the mangrove ecosystem is a source of important products to coastal populations in the form of poles and timber as building material for boats and houses, firewood, salt, tannins, dyes, charcoal, honey, wax, thatching and roofing materials and food (Macnae, 1968; Ong, 1982; Islam and Wahab, 2005; Hait and Behling, 2009).

Higher commercial fish catches are reported to be associated with mangrove habitats in many parts of the world (Hamilton and Snedaker, 1984; Pauly and Ingles, 1986; Singh *et al*., 1994). The higher standing stocks and high fisheries diversity linked with mangrove habitats have resulted in high commercial catches of fish and crustaceans (Hamilton and Snedaker, 1984; Staples *et al.*, 1985; Pauly and Ingles, 1986; Chong *et al.*, 1990; Morton, 1990; Robertson and Blaber, 1992; Singh *et al.*, 1994; Laegdsgaard and Johnson, 1995). Positive correlations between fisheries yield and the extent of mangroves have also been reported throughout the tropics (Staples *et al.*, 1985; Pauly and Ingles, 1986; Rönnbäck, 1999).

Mangroves are also important as sites for ecotourism and various scientific experiments (Kirui *et al.*, 2008). Thus, mangrove ecosystems along with their ecological functions provide various services (Kathiresan, 2005) and any loss of mangroves can result in a shortage of ecological subsidies to other habitats, lack of protection from extreme coastal hazards and imbalanced ecological functions.

1.1.4 Threats to Mangroves

Overexploitation and competition for coastal land are the primary factors that have reduced the area of mangroves (Wolanski *et al.*, 2000; Walton *et al.*, 2006). Diversion of freshwater for irrigation, construction of ponds for aquaculture purposes, land fillings for agricultural and various developments and construction of salt pans are also major threats (Linden and Jernelov, 1980; Nurkin, 1994; Primavera, 1995).

Changes in salinity and tides, excess sedimentation, altered soil physicochemistry, sewage disposal, industrial effluents, heavy metals, herbicides, acids and oil have had significant negative effects on the mangroves and are likely to intensify with increasing human populations (Kathiresan and Bingham, 2001; Alongi, 2002). The stress caused by the above factors increases the susceptibility of mangroves to diseases and pests particularly epidemics of bacteria, viruses, fungi, and boring insects and invertebrates that destroy leaves and wood (Alongi, 2002).

Natural disturbances of lightning, cyclones, hurricanes, tsunami and floods also result in long lasting damage to mangrove forests (Smith *et al*., 1994). Caribbean and Bay of Bengal mangroves are particularly damaged by hurricanes and cyclones (Kathiresan and Bingham, 2001).

Current mangrove areas in many countries are smaller than their original areas with a world average loss of 35% over the last 50 years (Valiela *et al.*, 2001). Conservation efforts are slow compared to the mangrove destruction and methodologies for sustainable harvesting are also still to be fulfilled (Kathiresan and Bingham, 2001). Mangroves often represent essential sources of income for poor families (Zorini, 2004), hence their destruction usually impacts disproportionately on the poor.

Changes in rainfall, temperature, atmospheric CO_2, sea-level, high water events, cyclones and storms as results of climate change are also likely to affect the structure and functionality of mangroves (Gilman *et al*., 2008). Particularly, the rising sea-level will flood some areas and may alter the competition between mangrove species, affecting the tree health, diversity and the area of mangroves (Gilman *et al*., 2007, Huxham *et al*., 2010).

1.1.5 Conservation, management and rehabilitation of Mangroves.

Disturbances to mangroves expose coastal areas to tidal inundations, wave actions, floods, storm surges and tsunamis increasing the threats to human safety and shoreline developments (Kathiresan and Rajendran, 2005; Dahdouh-Guebas *et al*., 2005;

Hashim *et al.*, 2010). Mangrove loss also affects coastal biodiversity and nursery habitats for fish eliminating numerous products and services for human communities (Mumby *et al.*, 2004; Gilman *et al.*, 2007).

The commonest strategy of conserving mangrove ecosystems is by the creation of protected areas in undisturbed sites (Field, 1998) whilst attempts have also been made for managing mangrove ecosystems for sustainable yield of natural products like timber, charcoal and shrimp (Robertson and Phillips, 1995; Chan, 1996). Although many of these attempts have ended in disaster due to poor management practices, the conclusion should not be that mangroves are impossible to be managed for sustainable natural products (Field, 1998). Rehabilitation of a severely destroyed mangrove forest back to its original state is difficult because the prior conditions that supported the forest to flourish are often difficult to restore (Islam and Wahab, 2005). However, the objectives of mangrove restoration projects are to restore the structure and functionality of a mangrove forest to a less disturbed condition (Hashim *et al.*, 2010). Although mangrove afforestation has been practiced for many years, information on the nursery rearing and planting techniques for mangrove species is still not adequate (Siddiqi and Khan, 1996; Kirui *et al.*, 2008). Identifying the causes of site degradation, assessing the site, sourcing of planting materials, monitoring outcomes and maintaining the resulting mangrove ecosystem are the key considerations for successful mangrove restoration while the long-term sustainability of the created mangrove forest is among the measures of success (Field, 1999). The knowledge of the benefits and values of mangroves must also be emphasized to the public including all the different stake holders and authorizers if the mangrove restoration project is to be successful (Shunula, 2002). Modern technological innovations like remote sensing coupled with aircrafts or satellites can overcome the ground difficulties although the costs of these applications may be unaffordable for small-scale restoration works (Field, 1999). Identification of genetically superior trees for micro, vegetative or seed propagations can also assist in mangrove restoration as indicated by Das *et al*., (1997) where they obtained significantly higher survival rates for 10 mangrove species planted in an arid site in India.

Large-scale mangrove plantings targeting conservation, fixation of increased atmospheric CO_2 and protection against natural hazards such as tsunamis face technical obstacles due to lack of knowledge regarding planting techniques (Siddiqi and Khan, 1996; Barbier, 2006) to produce better survival and accelerated biomass accumulation. Prior to the current work, there were no published accounts of properly controlled experiments on the effects of density on survival and growth of mangrove plants.

Due to the unavailability of information on how mangrove growth responds to density, mangrove replanting activities are carried out in varying densities, including ones that are likely to be sub-optimal leading to wasted time, money, space and planting materials. A properly controlled experiment to explore if facilitation (where high densities increase survival; Callaway and Walker 1997; Kirui *et al*., 2008) or competition (where high density causes self-thinning; Analuddin *et al*., 2009) predominate in mangroves would therefore provide information of practical as well as theoretical interest.

Proper studies on surface accretion (height increment of the sediment layer due to gradual deposition of sediment particles) and soil elevation (upward movement of soil due to some subsurface processes such as soil expansion and root growth) processes in mangroves may provide guidelines on manipulating the planting of mangroves to mitigate against the adverse effects of the rising sea-level as those two processes increase the height above the rising sea-level of mangrove sediment (Ellison and Stoddart, 1991; Gilman *et al.*, 2006; McLeod and Salm, 2006; McKee *et al.*, 2007; Gilman *et al.*, 2007, 2008) . The available literature on sediment accretion and surface elevation in mangroves (Chapman and Ronaldson, 1958; Cahoon and Lynch, 1997; Saad *et al.*, 1999; Krauss *et al.*, 2003; Rogers *et al.*, 2005; McKee *et al.*, 2007; Howe *et al.*, 2009; Krauss *et al.*, 2010) demonstrates wide variations between forest types, species, density and location. The majority of studies have been observational, without controls for location and other confounding variables. Particularly, there are no properly controlled and replicated studies on the effects of mangrove tree density on accretion and surface elevation processes. Since the density of mangrove forests partly determines the aboveground complexity and hence the accretion and elevation processes, results of a properly controlled mangrove density experiment should help understanding differences in sedimentation rates between different mangrove settings. Finding the relationship between the tree density and the accretion and elevation rates has obvious practical implications for managing the effects of sea level-rise.

Mangrove sediment provides food and habitats for various sediment invertebrates (Lee, 1998; Alongi, 1998) that are essential components of aquatic food webs as they are food for fish, invertebrates and birds (Sasekumar, 1974; Jones, 1984; Kathiresan and Bingham, 2001). Mangrove restoration activities should therefore aim to restore the faunal as well as the floral components of the ecosystem (Macintosh *et al.*, 2002). Restoration of full mangrove ecosystem functioning would imply achieving similar macrofaunal communities to those seen at reference sites. The floral density of mangroves could influence the macrofauna recruitment because the tree density will determine the rates of food supply (from litter fall) and the degree of shelter against desiccation (Ross and Underwood, 1997). Thus, high abundance and diversity of macrofauna at high mangrove densities might be expected. However, high organic enrichment in sediments coupled with poor oxygenation produces anaerobic chemical conditions or high levels of ammonia and sulphide (Magni *et al.*, 2009) reducing the species richness, diversity and biomass of benthic fauna (Pearson and Rosenberg, 1978). Moderate organic enrichment provides food to increase the abundance of marine benthos (e.g. McLusky, 1982; Majeed, 1987), hence the highest diversity and abundance of macrofauna can be expected at certain middle levels of tree density. The field of mangrove restoration still lacks this knowledge and a time series macrofauna study in different mangrove densities will help in filling this study gap.

Different sub components of sediments (silt, clay and sand) have different settling rates and the sediment textural pattern of tidal wetlands like mangroves vary according to physico-chemical parameters (Bhattacharya and Sarkar, 1996; Ramanathan *et al.*, 2009); and these textural variations have profound influences on marine chemical cycles (Ronnie and Middelboe, 2004; Jahnke, 2005). The distribution of different sediment types in mangroves and coastal wetlands depends on the energy conditions, wind and resistance to water flow imposed by plants (Yang *et al.*, 2008; Ramanathan *et al.*, 2009). The textural composition and the grain size distributions of coastal sediments influences the local biogeochemistry, nutrient, organic matter, water contents (Uncles *et al.*, 1998; Pasternack and Brush, 2001; Zhang *et al.*, 2002) and distributions of soft bottom fauna (Sanders, 1958; Woodin, 1978; Nel *et al.*, 1999; Ysebaert *et al.*, 2003; Atobatele *et al.*, 2005; Ikomi *et al.*, 2005). The varying density configurations inside natural mangroves may facilitate the deposition of different suspended components at different places in the forest as described by Yang *et al.,* (2008) however the effect of tree density on mangrove sediment texture has not been experimentally tested.

1.2 Aims and Objectives of the current study

The study of the role of mangrove planting density on sediment accretion, soil elevation, tree growth, biomass accumulation, faunal diversity, sediment texture, sediment carbon content and their sources is of interest for reasons of fundamental science, but may also provide guidance in the manipulation of mangroves in the face of sea-level rise and increased atmospheric CO_2. Such a detailed and controlled study is yet to be done and filling this study gap was the prime aim of the present study.

1.2.1 Aims

1) To examine the influence of mangrove planting density on a range of biological and physical responses, and to relate these findings to fundamental ecological science.

2) To derive appropriate lessons from these experiments for the guidance of mangrove planting and restoration projects, particularly in the face of sea-level rise and the importance of mangroves as carbon sinks.

1.2.2 Objectives

The objectives of the current study are the investigations of the effects of the mangrove density on;

1) Sediment accretion and soil elevation change compared to unplanted controls over time (Chapter II)

2) Survival, growth, biomass productions (aboveground and belowground) of mangroves in relation to sediment nutrient dynamics over time (Chapter III)

3) The changes of the community structure of sediment macrofauna compared to unplanted controls and natural mangroves over time (Chapter IV)

4) The sources and the storage of sediment carbon, changes of sediment texture compared to the unplanted controls (Chapter V)

5) Findings and overall conclusions (Chapter VI)

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CHAPTER 2- THE EFFECTS OF DENSITY ON SEDIMENT ACCRETION AND SOIL ELEVATION IN MANGROVES.

This chapter has contributed to the following two publications;

1) Huxham, M., Kumara, M.P., Jayatissa, L.P., Krauss, K., Kairo, J., Langat, J., Mencuccini, M., Skov, M. & Kirui, B. 2010. Intra and inter-specific facilitation in mangroves may increase resilience to climate change threats. Journal of Philosophical Transactions of the Royal Society B. 365: 2127-2135

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

2.1 Introduction

This section describes the evidence that mangrove destruction can cause coastal erosion. The mechanisms by which mangroves enhance sediment accretion and soil elevation and the effects of mangrove planting density on these two processes are also reviewed.

2.1.1 Mangroves and coastal protection.

Tsunami waves can be generated by underwater earthquakes, submarine landslides, volcanic activity or bolide impacts (Clague *et al.*, 2003) and the tremendous energy of these waves can cause disastrous damage to human life and properties (Tanaka, 2009). Mangroves provide protection against tsunami waves through absorption of the wave energy although the effectiveness depends on the wave magnitude, forest maturity and its configuration (Dahdouh-Guebas *et al*., 2005; Danielsen *et al*., 2005; Alongi, 2008; Tanaka, 2009). Similarly they can provide protection from destructive sea waves generated by other storm events (Badola and Hussain, 2005; Kerr and Baird, 2007; Mazda *et al*., 1997). High density forests of *Rhizophora* sp and *Avicennia* sp provided protection against tsunami events in India (Danielsen *et al*., 2005) implying the effectiveness of high density plantations of these species in areas susceptible to tsunami and storm events. However, any planting activities aiming to use high densities suffer from a lack of information on the effects of planting density on survival and growth of mangroves (Kumara, *et al*., 2010).

Coastal erosion exacerbated by intensive human activities (Cooper and McKenna, 2008) damages infrastructure and may require expensive mitigation strategies (Gillie, 1997; Weerakkody, 1997; Wiegel, 2002). It is a global issue causing widespread concern (Zhang *et al*., 2004; Airoldi *et al*., 2005; Cooper and McKenna, 2008; McKenna *et al*. 2009; Saengsupavanich *et al*. 2009) and may be much more severe with predicted sea-level rise (Phillips and Jones, 2006; Natesan and Parthasarathy, 2010). Coastal erosion can be controlled by natural beach vegetation such as mangroves; large scale coastal erosion due to the loss of mangroves has been reported in a number of studies. For example, the relationship between the presence of mangroves and changes in coastal area was assessed using remote sensing over a period of 30 years on the Thailand coastline, where the mangrove areas exhibited less erosion whilst non-vegetated segments or former mangrove areas showed considerable erosion (Thampanya *et al.* 2006). Thus, reductions in the prevailing erosion rates caused by the presence of mangroves were noted throughout this study. Similarly, deforestation of both F-type mangal (forest that is directly exposed to the open sea and thus exposed to sea waves) and adjacent R-type mangal (mangrove forest found on a flood plain along a tidal river that is inundated by most high tides) has caused large-scale coastal erosion in southern Vietnam since the early 20th century (Mazda *et al.* 2002). Human-mediated transition of mangrove forests to settlements, rice paddies, salt farms and aquaculture-ponds had caused an erosion rate of 50m/year in this coastal segment.

This ability to protect the coastline from erosion is mediated in part by the way in which mangroves dissipate wave energy. The dense networks of mangrove trunks, branches and especially aboveground roots that increase the bed roughness can dissipate the energy of incoming waves causing reduction of wave heights. Quartel *et al.* (2007) quantified the wave reduction and wave energy dissipation over an open tidal flat and within a neighboring mangrove area in the Red River Delta, Vietnam. The mangrove vegetation had a uniform flat bed consisting of 88.9% *Kandelia candel*, 7.4% *Sonneratia* sp. and 3.7% *Avicennia marina*. The wave energy decay and wave transformation models used for describing the hydrodynamics of the two areas showed higher wave height reduction (per meter cross-shore) in the mangrove than the sandy tidal flat surface. Furthermore, the resistance (drag force) exerted by mangroves was shown to depend on the species and the density of the vegetation. Each mangrove species has a unique configuration of trunks, prop roots and pneumatophores that exerts different drag forces and resulting different reduction rates of waves (Wolanski *et al.* 1999). The species possessing large pneumatophores exert higher drag forces on incoming waves than species such as *Kandelia candel* with no large pneumatophores (Furukawa and Wolanski 1996). The height reduction of waves increases with increasing density and height of the mangrove vegetation (Mazda *et al.* 1997).

2.1.2 Mangroves and coastal sedimentation

There is considerable scientific interest in sedimentation processes associated with mangroves, partly because of their importance in controlling coastal erosion and responding to rising sea-levels. The mechanisms of mangrove sedimentation, sediment accretion and sediment elevation will be reviewed under this section.

2.1.2.1 The mechanisms of Mangrove sedimentation

Mangroves provide a mechanism for trapping sediment, and thus mangrove forests are an important sink for sediment (Woodroffe 1992; Wolanski *et al.* 1992; Wolanski 1994; Furukawa *et al.* 1997). Mangrove forests catch sediment by their complex aerial root structures, thus potentially functioning as land builders (Chapman and Ronaldson 1958; Bird and Barson l977; Woodroffe 1992; Wolanski *et al.* 1992; Wolanski 1994; Furukawa *et al*. 1997; Krauss *et al*. 2003).

River discharge, the dumping of dredged material and the re-suspension of bottom sediment by waves and ships introduce suspended sediment into coastal areas

(Wolanski 1994) and the transport of that sediment into mangrove waters is driven mostly by local hydrodynamic rather than biological processes (Ayukai and Wolanski 1997).

Kathiresan (2003) found a significant difference in the concentration of suspended sediment between high and low tide waters in mangrove zones whilst such a situation was not recorded in non-mangrove areas. The mangrove zone had a high concentration of suspended sediments at high tide and low suspended sediment concentration at low tide, while estuarine proper and non-mangrove areas showed only very low concentrations of suspended sediments during both the tides. Kathiresan (2003) suggested that sediment particles are carried in suspension into mangrove forests at high tide, and they are maintained in suspension due to the turbulence caused by mangrove roots. At low tide, the concentration of suspended sediment in mangrove forests becomes less due to settlement facilitated by the slow movements of water during ebb tide. In this study, the change in suspended sediments between low and high tides was significantly greater in the mangrove-lined bank than that in the estuarine proper and the non-mangrove area suggesting that mangroves trap the suspended sediment at the low tide. He further described that the efficiency of sediment trapping varied with the types of mangrove zone: the *Avicennia-Rhizophora* interphase trapped 30% of total suspended sediment received at high tide while the *Avicennia* zone removed 25% and *Rhizophora* trapped only 20%.The high efficiency in trapping suspended sediment in the *Avicennia-Rhizophora* interphase was attributed to the widespread occurrence of numerous pneumatophores in *Avicennia* and to the prop roots of *Rhizophora.* This complex mix of aerial root types increased the surface area of the physical barrier that may have caused higher turbulence facilitating the sedimentation. However Kathiresan (2003) did not conduct an experimental study, and had no replication of his different zones; hence the effects reported may have been confounded by site conditions. The difference in sediment trapping between the two species may have been due to the fact that *Rhizophora* receives water with relatively higher velocity as it grows at the water-front, whereas *Avicennia* has lower velocity water as it occurs widely towards the top of the intertidal slope.

2.1.2.2 Previous studies on mangrove sedimentation

Surface accretionary processes have been studied at numerous mangrove sites globally (Chapman and Ronaldson 1958; Cahoon and Lynch 1997; Saad *et al*. 1999; Krauss *et al*. 2003; Rogers *et al*. 2005; McKee et at. 2007; Howe *et al*. 2009; Krauss *et al*. 2010) using the artificial marker horizon method. In this method, a recognizable artificial layer is established on the soil and it is left to allow the free settlement of sediment. The thickness of sediment above the marker is measured and the readings are converted to a sedimentation rate such as mm yr^{-1}. Various materials have been used as the marker such as brick-dust (Chapman and Ronaldson1958) Perspex (Saad *et al.*1999) carbonate sand (McKee *et at.* 2007a) and feldspar (Cahoon and Lynch 1997; Krauss *et al*. 2003; Rogers *et al*., 2005; Howe *et al*. 2009; Krauss *et al*. 2010). Bird (1971) and Spencely (1982) have utilized stakes or pins for the same purpose. This method involves fixing vertical rods in the field leaving a measured height above the ground and the sediment accumulation is measured as the reduction of the above-ground height. More advanced isotopic and radiocarbon methods also have been utilized for the detection of vertical sediment accretion rates in some studies (DeLaune, *et al,* 1978; Stevenson *et al.* 1985; Onema, 1988; Lynch *et al.* 1989).

Vertical sediment accretion rates as measured using a number of different marker horizons from various mangrove systems throughout the world are listed in Table 2.1.

The height above sea level of sediment is increased by two processes namely vertical accretion and soil elevation (Ellison and Stoddart 1991; Gilman *et al*. 2006; McLeod and Salm 2006; McKee *et al.* 2007). The first refers to the height increment of the sediment layer due to gradual deposition of sediment particles carried by water whilst soil elevation refers to the upward movement of soil due to some subsurface processes such as soil expansion and root growth.

Saad *et al.* (1999) recorded mean annual accretion rate of 10.6 mm yr^{-1} in Malaysian mangroves, with 2.6 mm $month^{-1}$ and 1.2 mm $month^{-1}$ accretion rates for the monsoon period and the non monsoon period respectively. The vertical accretion was measured as the rate of accumulation above slabs of Perspex (9cm x 9cm x 1.5mm) placed at recorded depths to act as marker levels. Although this study provides sediment accretion rates in a natural mangrove forest and its response to monsoon changes, it suffers from two major shortcomings. First, it did not consider the effects of species composition and the density of mangrove trees on sedimentation, which would help in comparing with the accretion rate of other mangrove forests of known diversity and tree densities. Second, the accretion rates in mangrove forests were not compared with the accretion rates of adjacent non-mangrove areas as controls.

Table: 2.1 Vertical sediment accretion rates as measured using a number of different marker horizons from various mangrove systems throughout the world.

Study	Marker horizon	Accretion rate (mm yr^{-1})	Site
Chapman and Ronaldson (1958)	Brick dust	1.0	New Zealand mangrove
Cahoon and Lynch (1997)	Feldspar	4.6 -7.8	South-western Florida
Saad *et al*. (1999)	Perspex	6.4 -14.6	East coast of Peninsular Malaysia
Krauss *et al*. (2003)	Feldspar	7.2 -11	Kosrae and Pohnpei Islands, Micronesia
Rogers *et al.* (2005)	Feldspar	2.6 - 7.1	Australia
McKee *et al*. (2007a)	Carbonate sand	0.7 - 3.5	Belize
Howe *et al*. (2009)	Feldspar	1.8 – 2.8	Western Australia
Krauss *et al*. (2010)	Feldspar	2.9 – 20.8	Kosrae and Pohnpei Islands, Micronesia

Cahoon and Lynch (1997) made simultaneous measurements of vertical accretion and soil elevation in fringe, basin and overwashed island mangrove forests located in South-western Florida. The mangrove species composition of the fringe was mostly dominated by *Rhizophora mangle* and the basin forest composed of a mixture of *Rhizophora mangle* and *Avicennia germinalis* while the island forests included monospecific stands of *Rhizophora mangle*. The study highlighted the importance of both surface (sediment accretion) and subsurface (soil compaction, soil expansion) processes on the vertical development of mangrove soil. The vertical accretion was measured as the rate of accumulation above Feldspar marker horizons while the soil elevation changes were recorded with Sediment Erosion Table (SET), which is a portable levelling device designed to attach to a benchmark pipe driven in to the soil. This study utilised two measurements to calculate amounts of shallow subsidence (accretion minus elevation change) in each mangrove forest and the recorded rate of shallow subsidence was consistently 3-4 mm yr^{-1} in the fringe and overwash island forest but was negligible in the basin forest. The study compared the three different mangrove forest types showing that both surface and subsurface processes that control soil dynamics can differ among mangrove forest types.

Krauss *et al.* (2003) used feldspar marker horizons and sediment pins to investigate the influence of three different mangrove root types - prop roots in *Rhizophora* sp., root knees in *Bruguiera gymnorrhiza,* and pneumatophores in *Sonneratia alba* - on vertical accretion and elevation changes in three mangrove forests in Micronesia. The “accretion” that was referred to the resultant measurements of the previous sediment pins or stake studies was here distinguished between the processes of vertical accretion and elevation.

They referred to vertical accretion only when discussing the results of the feldspar marker horizon technique as this method can only measure positively accreted sediments. Since an inserted pin reflects not only vertical accretion and erosion but also sub-surface processes down to the bottom of the inserted pin (e.g. shallow subsidence) they referred to pin measurements as elevation change.

In each of three different mangrove zones, fringe, interior and riverine mangroves, three $1m^2$ areas, one with mostly prop roots, one with mostly pneumatophores and one with mostly root knees were selected while a fourth area was created by cutting all roots and exposing bare soil. The prop roots facilitated vertical accretion (11.0mm year^{-1}) more than pneumatophores (7.2mm year^{-1}), root knees (9.2mm year^{-1}) or bare soil (9.4 mm year^{-1}) while the sediment elevation increased at an average rate of 1.3 mm year^{-1} across all root types with rate difference by root type, ranging from 0.2 to 3.4 mm year^{-1}. The prop roots assisted in the settling of suspended sediments from estuarine water but prop root structures were not as successful as pneumatophores in maintaining sediment elevation.

Rogers *et al.* (2005) demonstrated that both groundwater recharge and belowground biomass production can influence surface dynamics where these processes are more complex than soil accretion and soil autocompaction alone. This study followed the dieback of an anterior portion of an Australian mangrove forest, utilizing Surface Elevation Tables and Feldspar marker horizons in the impact, intermediate and controlled forests to measure vertical accretion, elevation changes and shallow subsidence. During strong vegetative regrowth in the impact forest, surface elevation increase had exceeded vertical accretion apparently as a result of belowground biomass production. In addition, surface elevation in all forest zones showed a correlation with total monthly rainfall during a severe *El Niňo* event, highlighting the importance of rainfall to groundwater recharge and surface elevation. The recorded surface elevation rates for Impact forest, Intermediate forest and Control forest were 2.9, 4.2, 7.2 mm yr^{-1} respectively.

McKee *et al.* (2007) studied the contributions of root matter to mangrove soil elevation change in natural *Rhizophora mangle* in the islands on the Caribbean coasts of Belize, Honduras and Panama. They specifically tested the hypothesis: the accumulation of refractory mangrove roots contributes directly to soil volume and hence elevation. The effects of nutrient additions on root growth were also investigated. For a 3 year study period, they found that the addition of nutrients to mangroves caused significant changes in rates of mangrove underground root accumulation, which influenced both the rate and direction of change in elevation. Areas with low underground root input lost elevation and those with high rates gained elevation indicating the addition of N or P alters vertical land building in mangroves. The study resulted in elevation change ranging from -7.7 to 8.4mm yr^{-1} across the 27 experimental plots while the surface accretion, above marker horizon, ranged from 0.7 to 3.5 mm yr^{-1}.

Krauss *et al.* (2010) investigated sediment accretion and soil elevation dynamics of mangrove forests in the islands of Kosrae and Pohnpei, Federated States of Micronesia (FSM). Surface accretion rates ranged from 2.9 to 20.8 mm y^{-1}, and were high for natural mangroves while the elevation change ranged from -3.2 to 4.1 mm y^{-1} over a period of 6.5 years.

The literature on sediment accretion and surface elevation in mangroves hence demonstrates that differences between forest types, species, density and location may all contribute to the wide variations recorded in both of these factors. The majority of studies have been observational, without controls for location and other confounding variables. There are no properly controlled and replicated studies on the effects of mangrove density on sediment and surface elevation processes, and conducting such a study was one of the objectives of the current work.

2.1.3 Rationale for current study

The density and the type of species of trees of any natural forest decide it’s structure and thus natural mangrove forest structure can be highly variable even within the same geographical locality. The sedimentation rate on the other hand can also vary among different forest structures because the forest structure obviously decides the magnitude of bed roughness which directly controls the sediment accumulation. Thus, it is obvious that in any mangrove sedimentation study, the tree density and tree diversity should be considered as a part of the study if the findings are to be used for meaningful comparisons with other mangroves.

The available literature on sediment accretion and surface elevation in mangroves demonstrates that differences between forest types, tree species, tree density and location may all contribute to the wide variations recorded in both of these factors. More importantly, no studies have explored the effects of mangrove density on sedimentation using properly controlled experiments with planted trees and unplanted controls. The majority of all the sedimentation studies have been observational, without controls for location and other confounding variables. This implies the need for properly controlled and replicated studies on the effects of mangrove density on sediment accretion and surface elevation processes, and conducting such a study is one of the aims of the current work. Furthermore, no mangrove sedimentation studies have been published so far in Sri Lanka and therefore the findings of this study will also be useful for local management purposes.

2.1.4 Aims and objective of the current study

Therefore the aims of the current study are: Conducting a properly controlled mangrove density experiment with sufficient numbers of replicates and publishing the findings on the sediment accretion and soil elevation in different mangrove densities. This publication is aimed to guide future mangrove replanting activities for mitigating the effects of sea-level rise on mangroves and preventing coastal erosion.

The objectives are:

1) Conducting a three year long mangrove density experiment with sufficient numbers of treatments and replicates.

2) Collection of accretion and soil elevation data periodically.

3) Analysis of data for comparing sediment accretion and soil elevation between different mangrove densities and unplanted controls.

2.1.5 Null and alternative hypothesis for the current study

The following hypothesis will be tested in this part of the study.

Null hypothesis: Sediment accretion and soil elevation are independent of mangrove density

Alternative hypothesis: Sediment accretion and soil elevation depend on mangrove density

2.2. Materials and methods

2.2.1 Study site and experimental design

The study site was located at Palakuda, situated in Puttalam Lagoon, on the west coast of Sri Lanka (Figure 2.1: 8.08° N; 79.73° E). Maximum tidal range in the lagoon is 60 cm with high tides twice per day on average. Between June and October the site remains mostly inundated even at low tide, but is exposed from November to May as the prevailing direction of wind changes.

The surface area of the Puttalam Lagoon is around 400 km^2 and it is generally very shallow (1-2m), except in the central furrows of the lagoon where depth reaches 5 m. The lagoon receives two major perennial freshwater inputs from the Kala Oya and Mee Oya Rivers (Figure 2.1). The salinity of the lagoon varies from oceanic levels (~35 ppt) at the Northern outlet to 0 ppt at river discharge points to hypersaline in the extreme Southern portion of the lagoon (Johnson and Johnstone, 1995). Salinity averaged 23 ppt at the field site (pers. ob.). The lagoon is rich in fish, shellfish, saltmarsh vegetation and mangroves. Since some areas of the lagoonal coast have been used for shrimp farms, salt pans, coconut farms, human settlements, boat landings and road construction, the mangrove woodland is not continuous but exists in patches around the lagoon.

Rhizophora mucronata is a mangrove species distributed from east Africa, throughout Australasia, and into the western Pacific Ocean (Duke *et al*. 2002), and is common in Sri Lankan mangroves (Jayatissa *et al*. 2002); it occurs naturally at the experimental site. The species grows tall (around 25m) producing large numbers of prop roots and it shows viviparicy resulting in stick-like propagules (Kathiresan and Bingham 2001). Propagules from *R. mucronata* are large (up to 80 cm in length: Duke 2006), and were collected from wild trees to plant on an open mudflat. The mudflat had no any previous record of mangroves possibly due to lack of seed supply from the natural forest. The directions of waves and the tide do not support transporting seeds in to the mudflat for recruitments.

Fifteen 7.2m × 7.2m plots, arranged in three blocks of five treatments each, with a minimum gap of 1.2 m between plots, were demarcated in May 2006. Plots were randomly assigned to one of five treatments within each block, which included four planting densities (6.96, 3.26, 1.93 and 0.95 *R. mucronata* seedlings m^{-2}) and an unplanted control (0 seedlings m^{-2}). Planting densities equated to 361, 169, 100, 49 and 0 seedlings per treatment). Hence, each treatment was replicated three times within a randomized block design (figure 2.2).

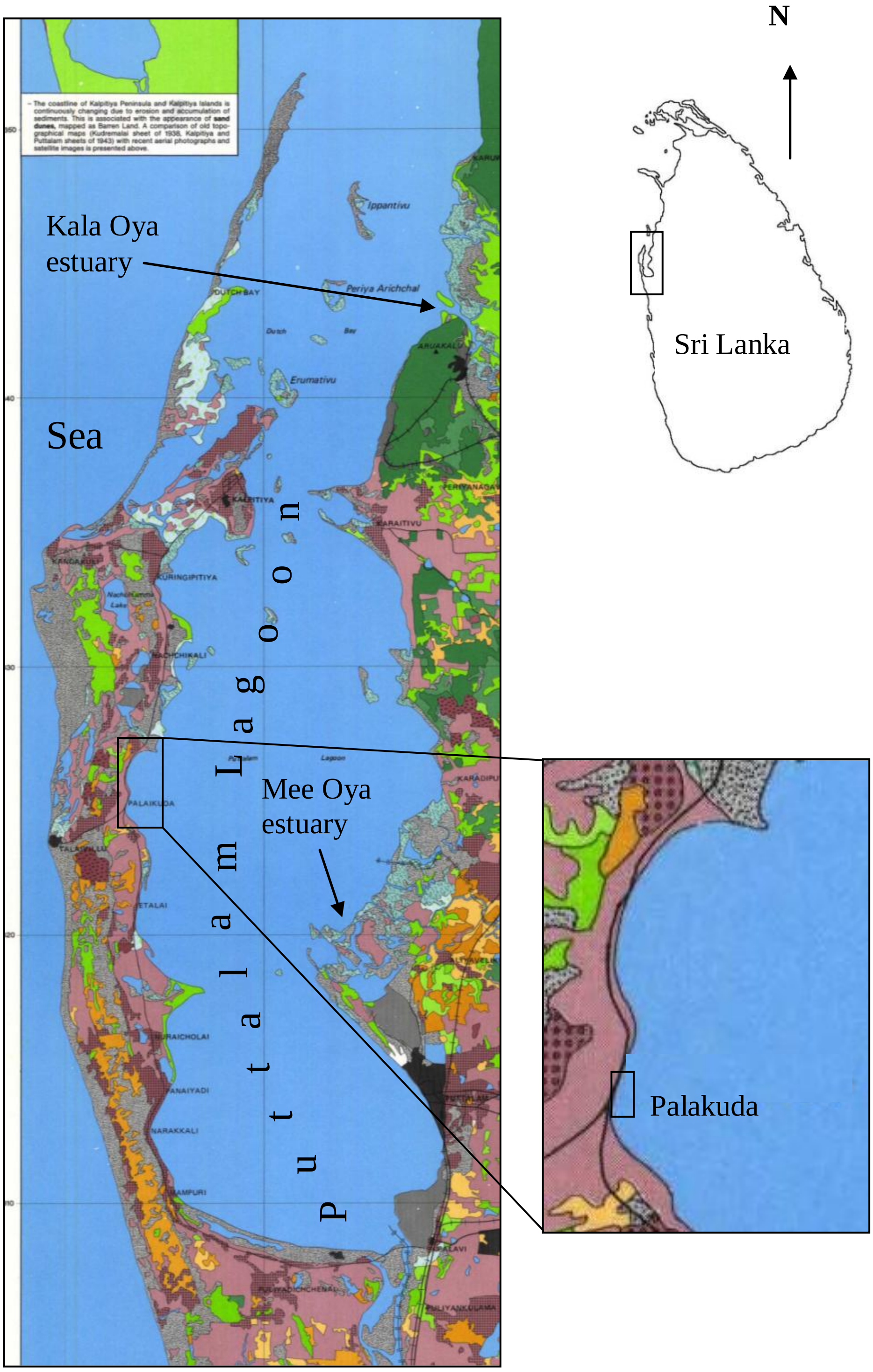

Figure: 2.1: Location of Palakuda within Puttalam Lagoon in Sri Lanka where the experimental plots were established. (Source: Survey Department of Sri Lanka)

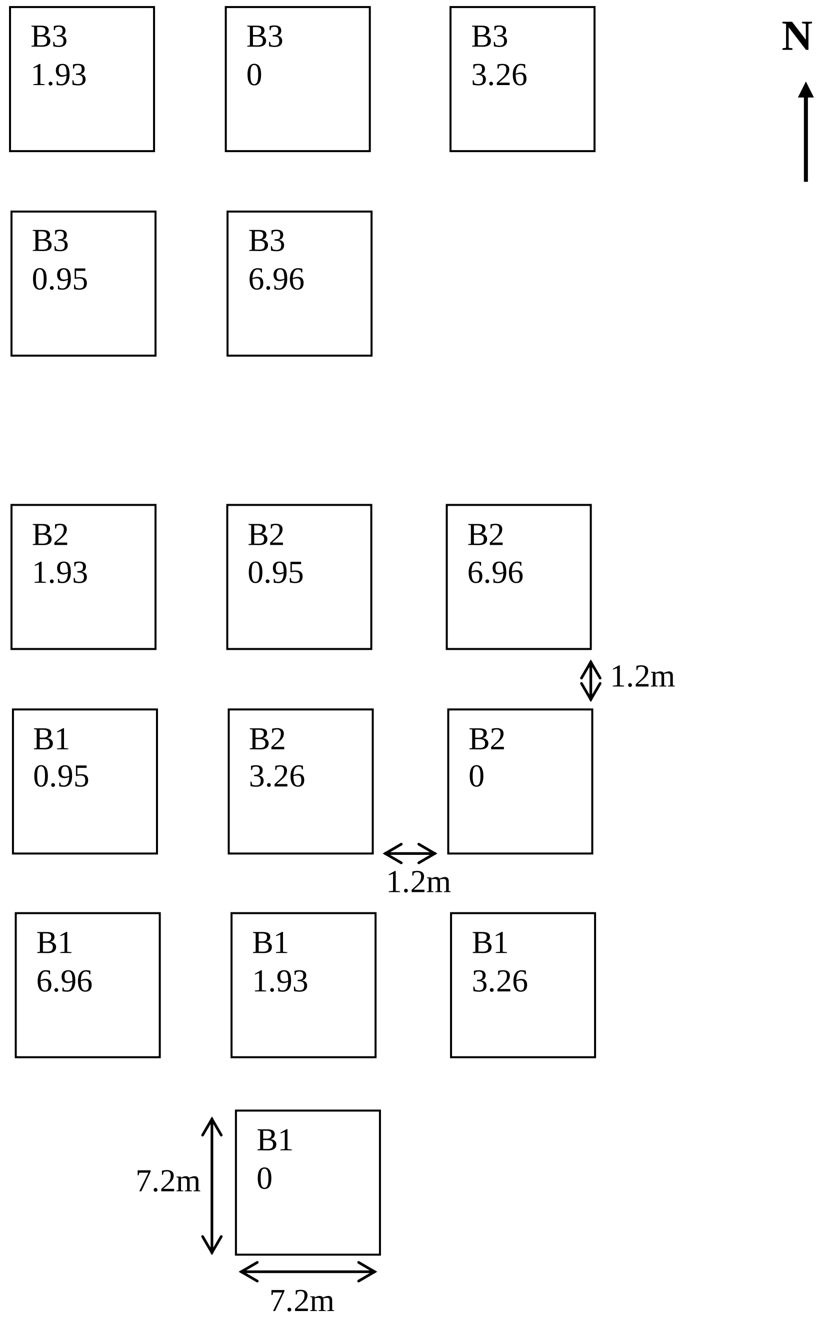

Figure: 2.2: Experimental plot layout of different densities of *R. mucronata* seedlings planted in Palakuda, Puttalam Lagoon, Sri Lanka. (B1 to B3=experimental blocks; 6.96 to 0 indicates the planting densities of trees m^{-2}).

a

b

c

d

Figure: 2.3 Palakuda experimental site, Puttalam Lagoon, Sri Lanka. (a- Planting of *R. mucronata* seedlings in 2006. b,c,d represents the tree growth in plots by 2007, 2008,and 2009 respectively).

2.2.2 Sediment Accretion and Surface Elevation

Changes in height above sea level of the soil surface in mangroves are assessed by measuring two main processes: vertical accretion and surface elevation change. Vertical accretion refers to the gradual deposition of sediment particles carried by water, whilst surface elevation change refers to the upward movement of sediment due to a combination of vertical accretion and subsurface processes such as shallow soil subsidence and sediment expansion (Cahoon and Lynch 1997). Vertical sediment accretion was determined by laying a mixture of 50% powdered feldspar and 50% sand over a 30-cm × 30-cm surface area in the centre of each treatment (Cahoon and Lynch, 1997). Accretion was periodically measured from sediment plugs, 1-cm^2 × 5-cm deep, cut out of the sediment containing the marker horizon, as the distance from the top of the plug to the feldspar marker horizon with 0.1 cm accuracy. Four sediment plugs were measured and averaged to give a single reading for each treatment at each sampling time. Cumulative accretion values and annual accretion rates were calculated for each treatment.

Elevation change was measured simultaneously with accretion measurements by using sediment pins (sensu Krauss *et al*. 2003), with elevation in this case representing the net effect of vertical accretion along with all shallow root zone processes to a depth equal to that of the pin. At the two opposite corners of the feldspar marker-horizon in each treatment, two 1-m long × 0.64-cm diameter stainless steel pins were driven 80 cm into the soil, placing pins approximately 30 cm apart. In general, as long as pins are placed 10 cm apart or more, their interactive effects on the measurement of sediment retention are negligible (Spenceley, 1977). The distances from the top of each pin to the sediment surface were measured to the nearest 0.1 cm using a standard ruler and these were averaged to give a mean pin height per treatment for each time interval. Data were used to calculate cumulative and annual increments from May 2006 to August 2009 from all treatments.

2.2.3 Statistical analyses

Data were examined for normality and homoscedasticity of residual variances and transformed where necessary. Repeated measures ANOVA (with treatments as the between-factor variable and time as the within-factor variable) was used to compare the rates of sediment accretion and surface elevation over time, after checking for sphericicity. Mean annual vertical accretion rates and mean annual surface elevation change were compared between the treatments using two-way ANOVA (with blocks and treatments as factors) tests. All the statistical analyses were carried out with Minitab, Version 14.20 (Minitab Inc., State College, PA, USA) or SPSS, Version 13.0 (SPSS Inc., Chicago, IL, USA) statistical packages.

2.3 Results

2.3.1 Vertical Accretion

Accretion rates varied significantly by time and among plantation densities (Table 2.2; Figure 2.4). However there was also a highly significant interaction term between these factors. Interpreting the results for main factors is complicated when there are significant interactions; a common approach is to conduct separate ANOVAs for each level of the within-subject variable, but this can result in inflated type 1 error and a confusing proliferation of results (Underwood, 1997). Instead, we analysed the composite variable of annual vertical accretion rates using two-way ANOVA (with blocks and treatments as factors). Accretion differed significantly between treatments (Table 2.3) but not between blocks. Accretion increased with increasing seedling density, with values (mean ± S.E.) of 13.0 (± 1.3), 10.5 (± 0.9), 8.4 (± 0.3), 6.9 (± 0.5) and 5.7 (± 0.3) mm yr^{-1} for treatments of 6.96, 3.26, 1.93, 0.95, and 0 seedlings m^{-2}, respectively (Table 2.4). However, accretion rates in all the treatments showed a reduction after 593 days (Figure 2.2). The highest plantation density (6.96 seedlings m^{-2}) trapped more sediment than any other treatment.

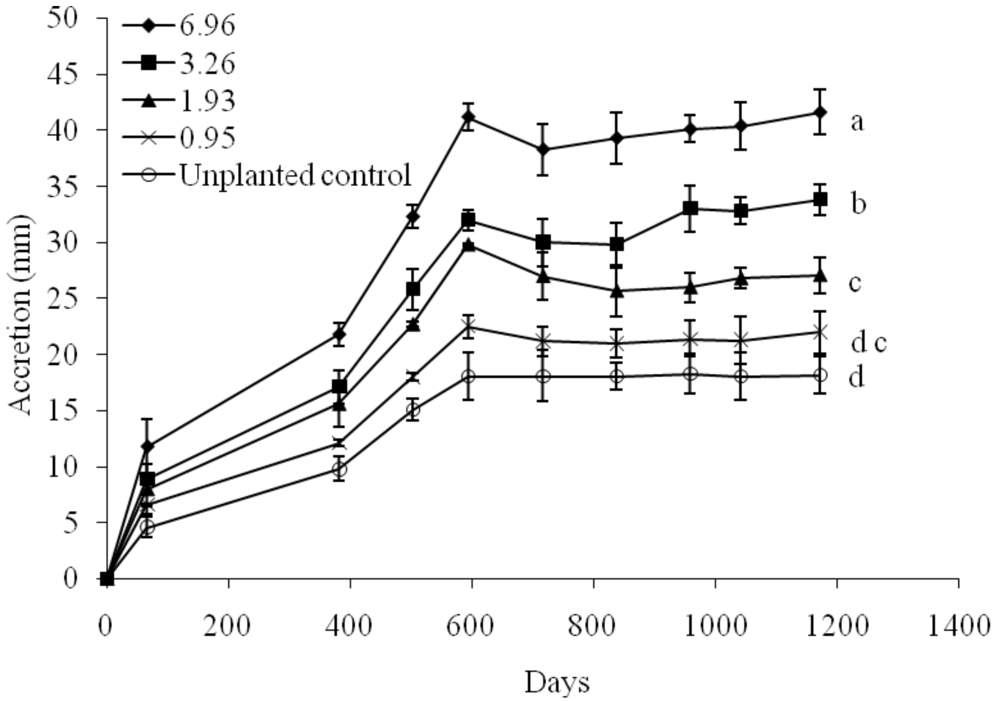

Figure: 2.4. Mean (±S.E.) cumulative surface accretion at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Lines represented by different letters identify significantly different mean annual accretion rates at α = 0.05. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

Table: 2.2. Repeated measures ANOVA for annual sediment accretion rates by different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Time	9	1765.25	870.01	<0.001
Treatment	4	1383.66	12.93	<0.001
Time × Treatment	36	34.36	17.03	<0.001
Error (Time)	90	2.03		
Error (Treatment)	10	10.94		
Total	149	3196.14		

Table: 2.3. Two-way ANOVA for annual sediment accretion rates by different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Treatment	4	26.86	12.12	0.001
Block	2	0.77	1.48	0.283
Error	8	0.52		
Total	14			
S = 0.72; R-Sq = 96.31%; r-Sq (adj) = 93.54%				

Table: 2.4. Mean annual sediment accretion rates (mm yr^{-1} ± SE) by different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Density of *R. mucronata* (Seedlings m^{-2})	Annual sediment accretion rates (mm yr^{-1} ± SE)
6.96	13.0 ± 1.3
3.26	10.5 ± 0.9
1.93	8.4 ± 0.3
0.95	6.9 ± 0.5
Unplanted control	5.7 ± 0.3

2.3.2 Elevation Change

Repeated measures ANOVA showed that elevation rates also differed significantly among different mangrove densities and times but again there was a significant interaction (Table 2.5; Figure 2.5). Two-way ANOVA on mean annual surface elevation change showed significant differences among mangrove densities but not among blocks (Table 2.6). For the highest density of 6.96 seedlings m^{-2} elevation was 2.8 mm yr^{-1} (± 0.2) while rates of elevation change for 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were 1.6 (± 0.1), 1.1 (± 0.2), 0.6 (± 0.2), and -0.3 (± 0.1) mm yr^{-1}, respectively (Figure 2.5: Table 2.7). Tukey`s comparisons showed a ranking of elevation change among mangrove plantation density similar to that of accretion (Figure 2.4 vs. Figure 2.5), suggesting that density is controlling both accretion and sediment surface elevation change relative to a depth of at least 80 cm on these plantation sites.

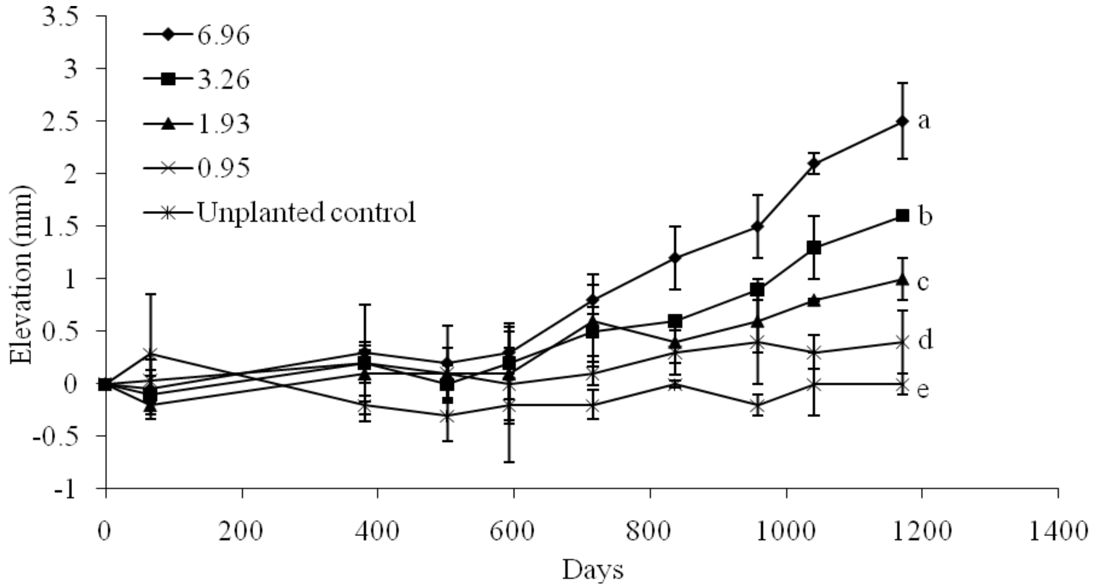

Figure: 2.5. Mean (± S.E.) cumulative surface elevation change at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Lines represented by different letters identify significantly different mean annual rates of surface elevation change at $\alpha = 0.05$. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

Table: 2.5. Repeated measures ANOVA for annual sediment elevation by different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Time	9	2.17	9.85	0.001
Treatment	4	4.69	26.39	0.001
Time × Treatment	36	0.53	2.37	0.001
Error (Time)	90	0.22		
Error (Treatment)	10	0.17		
Total	149	7.80		

Table: 2.6. Two-way ANOVA for annual sediment elevation by different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Treatment	4	3.69	4.4	<0.001
Block	2	0.01	0.41	0.681
Error	8	0.03		
Total	14			
S = 0.18; R-Sq = 98.35%; r-Sq (adj) = 97.11%				

Table 2.7 Mean annual sediment elevation rates (mm yr-^{1} ± SE) by different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Density of *R. mucronata* (Seedlings m^{-2})	Annual sediment elevation rates (mm yr^{-1} ± SE)
6.96	2.8 ±0.2
3.26	1.6 ±0.1
1.93	1.1 ±0.2
1.2	0.6 ±0.2
Unplanted control	-0.3 ±0.1

2.4 Discussion

Our study found higher accretion rates at greater mangrove plantation densities. This result supports the work of Young and Harvey (1996), who found increased sediment accretion at greater densities by using artificial structures (i.e., small apple tree cuttings) to simulate the pneumatophores of *Avicenna marina* in a rapidly accreting New Zealand estuary. Mangrove sediment accretion is mostly controlled by physical processes such as the input of suspended sediment, the magnitude of water movements, and flocculation and settling under gravity, although the capacity for overall soil building in mangroves may be related as much to belowground biogenic processes in some environments (McKee *et al*. 2007).

Fine cohesive sediment particles are carried in suspension into mangroves at high tide, maintained in suspension due to the turbulence caused by mangrove roots when water movement is rapid, and then settle to the bottom during ebb tide when water movement is slower and the turbulence vanishes (Saad *et al.* 1999; Kathiresan 2003). Thus, greater numbers of stems and their associated roots promoted a correspondingly high aerial root density at the plot-level in our high density treatments and facilitated the trapping and binding of sediment through increased friction during ebb, and perhaps flow, of tides. The positive relationship between density and accretion rates found in the current study suggests that any increased turbulence caused at higher plantation and aerial root densities (sensu Furukawa and Wolanski 1996; Krauss *et al.* 2003) is obviated by increases in sediment trapping during slow water flow. However, mangroves in Puttalam Lagoon are exposed to microtidal ranges (up to only 60 cm), and thus are expected to harbor less potential for turbulence-induced erosion than other systems studied (e.g. Australia and Micronesia).

There was a clear decrease, or stasis for treatments of 0 seedlings m^{-2}, in sedimentation rates among all treatments after 593 days (Figure 2.4). The reason for this is not altogether clear. Because a reduction in the accretion trajectory occurred in the unplanted control as well as in the planted treatments, a biological cause is unlikely. Rather, this apparent anomaly could reflect a change in the suspended sediment supply to Puttalam Lagoon. This variability over time emphasizes the importance of long-term monitoring for determining accurate annual rates of mangrove sediment surface vertical accretion and elevation change. What is more intriguing is that mangrove sediment surface elevation change among treatments also began to chart different trajectories around this same time frame (Day 563), perhaps reflecting a shift in dependence on belowground root contributions as mangroves produced greater biomass and accretion normalized. Consistent fluctuations in elevation increment among treatments in this fashion are not always described for mangroves, but the effects are reported with a high enough frequency in the literature to indicate that regional processes (e.g., ENSO, tropical storms, reductions in rainfall) sometimes supersede local effects in controlling elevation dynamics, e.g., south Florida, USA (Whelan *et al*. 2005), Australia (Rogers and Saintilan 2008), Micronesia (Krauss *et al*. 2010), among others.

Furthermore, accretion rates in the highest density treatment of the current study ranks among the second highest reported in the literature to date, indicating that we can mimic a full range of mangrove accretion rates through artificial manipulation of plantation densities. In fact, our study is the only sediment accretion and elevation study in planted mangroves to date whilst all other studies have taken place in various natural mangrove settings. Since many factors will influence accretion, there are many possible explanations for the wide range of values reported; however, it is likely that the high densities in our study were a key reason for the relatively high accretion rates. Likewise, studies from natural mangrove ecosystems do not always assess the density of mangrove shoots or roots, but it is likely that root densities confound relationships that are perhaps attributed to other sources in those studies, such as hydrogeomorphic zone. For example, prop roots associated with *Rhizophora* accreted sediments at a rate of 11 mm yr^{-1}, but were not as effective as *Sonneratia* pneumatophores in retaining these sediments to promote positive elevation increment over time, even though sediments accreted at only 7.2 mm yr^{-1} in *Sonneratia* pneumatophores (Krauss *et al*. 2003). It is likely that a greater proportion of *Rhizophora* versus *Sonneratia* trees in the overstory in this case will trigger different accretion and elevation processes regardless of where trees are located. There was a large contrast between the high rates of accretion and the relatively low rates of overall surface elevation change as measured by the pins in Puttalam Lagoon; in the case of the control, an accretion rate of nearly 6 mm yr^{-1} corresponded to a mean reduction in surface elevation of 0.3 mm yr^{-1}. Hence it is clear that accretion rates alone provide an incomplete indicator of surface elevation change.

2.5 References

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CHAPTER 3- EFFECTS OF DENSITY ON GROWTH AND BIOMASS PRODUCTION IN PLANTED MANGROVES

This chapter has contributed to the following two publications;

1) Huxham, M., Kumara, M.P., Jayatissa, L.P., Krauss, K., Kairo, J., Langat, J., Mencuccini, M., Skov, M. & Kirui, B. 2010. Intra and inter-specific facilitation in mangroves may increase resilience to climate change threats. Journal of Philosophical Transactions of the Royal Society B. 365: 2127-2135

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

3.1 Introduction

This section focuses on survival, growth and biomass production in relation to mangrove planting density. Changes in root morphology under different planting densities are also documented.

3.1.1 Growth and Survival of planted Mangroves

Mangrove trees could be planted at a range of densities and in high density cases, the growth and survival of trees may be compromised because of crowding effects. For example, Analuddin *et al*. (2009) described self-thinning in crowded mangrove stands of *Kandelia obovata*, a process widely described in the forestry literature. However, it is also possible that high density conditions could enhance survival and growth; this may be particularly true for plants growing in stressed environments (Callaway and Walker, 1997; Kirui *et al.*, 2008). Denser mangrove stands or alternate vegetation types may facilitate mangrove stand regeneration, sediment accretion, and elevation gain, as previously described by a number of mechanisms (McKee *et al*. 2007; Gedan and Silliman 2009; Huxham *et al*. 2010). Hence, there is potential for a conflict in management objectives when planting mangroves; enhancing density may result in faster sediment accretion and positive surface elevation increment, but could also lead to higher mortality caused by competition. In this study, the roles of facilitation and competition on seedling growth and survival associated with different mangrove plantation densities are investigated. Furthermore, the growth of the mangrove under high densities could be affected by limited light where, the optimal density in natural mangroves depends on species requirements for light (eg: *Rhizophora* sp is the most shade-tolerant species) (Imbert *et al.*, 2000). Mangrove growth also depends on the supply of soil nutrients particularly N and P (Boto and Wellington, 1984; Feller, 1995; Lovelock *et al*., 2007) and high competition for soil nutrients at higher densities would limit the tree growth unless there are compensatory mechanisms that fulfil the higher demand. Time series growth and survival data from high density replicates will help address these questions and filling this study gap is also among the objectives of the current study.

There are no published, controlled studies on the effects of tree density on mangrove survival and growth, and experimental field studies on mangrove mortality in general are rare. Berkeley and Perry (2008) studied three embayments with differing *Rhizophora mucronata* planting histories (Baie Diamant – planted in the period 1990 and then again in 1995 and 1996; Anse Pansia – planted during the period 1995-1997 and then again in 2001; and Anse Goeland – planted in 2001) in the North-West coast of Rodrigues, in the South Western Indian Ocean. Mangroves were rapidly developed at Baie Diamant where tree and sapling densities in the mangroves were up to ~6 per m^2 and the mangroves showed clear signs of seaward propagation and active juvenile establishment. At Anse Pansia mangroves were also establishing well although tree densities were far lower (~1.5 trees or saplings/m^2). At Anse Goeland – essentially a control site - the mangroves were very patchy and stunted. Although this study deals on the mangrove planting density, it suffers lack of a proper design with sufficient replicates and also the publication lacks more details because it is an abstract.

3.1.2 Biomass production in Mangroves.

The total biomass of mangroves includes both aboveground and belowground components; studying the latter is rather difficult due to muddy conditions, heavy wood and intensive labor (Komiyama *et al.*, 2008). Therefore, most of the mangrove biomass studies have focused on relatively easy aboveground elements (Tamooh *et al.*, 2008).

3.1.2.1 Aboveground Biomass.

Three main methods are used in forest aboveground biomass studies: the harvest method (destructive harvesting and measuring the tree biomass), the mean-tree method (measuring the biomass of a representative in homogeneous forests) and allometry (use of allometric equations produced from the dry weights of few individuals). Since mangroves are conserved forests, the destructive method may not be practicable while the heterogeneity of most mangrove forests excludes the mean-tree method (Komiyama *et al.*, 2008). Therefore, the allometric methods have commonly been used in mangrove aboveground studies that involve the use of regression equations (produced from harvesting a few selected individuals of a range of heights or diameters) to convert the tree height or diameter into the biomass (Komiyama *et al.*, 2008). However, the site and species specific dependency of these equations cause problems in repeated uses at different sites. Aboveground biomass productivity has been estimated principally in natural mangrove stands (e.g. Clough, 1992; Komiyama *et al.*, 1987; Fromard *et al.*, 1998; Komiyama *et al.*, 2002; Soares and Novelli, 2005; Zianis and Mencuccini, 2003) with fewer studies in planted stands (e.g. Kairo *et al.*, 2008; Tamooh *et al.*, 2008). The measured mangrove aboveground biomasses both in natural and planted mangroves vary between 0.73 to 43.6 kg m^{-2} globally (Komiyama *et al.*, 2008). The variance of forestry factors, including diversity, tree density, age, the level of disturbances and growth rates, along with between site variations such as latitude, have resulted in this large variance between different mangroves.

3.1.2.2 Belowground Biomass.

Mangrove belowground biomass studies are important in terms of understanding the nutrient turnover and potential to store carbon (Tamooh *et al.*, 2008). Mangrove belowground biomass increases with age of the trees but the root density decreases with the soil depth (Tamooh *et al.*, 2008). Extraction of mangrove belowground biomass involves trench (e.g.Tabuchi *et al.*, 1983) or soil coring (e.g. Briggs, 1977;

Mackey, 1993, Alongi *et al*., 2000) methods. The relatively soft mangrove substrate facilitates taking soil cores and hence studying the distribution of roots with soil depth (Komiyama *et al*., 1987). The mangrove roots can be categorized in to various sub groups (e.g. Tamooh *et al.*, 2008) however they can be broadly categorized in to three basic classes as fine, medium, and coarse. Studying the fine root distribution can reflect the spread of soil nutrients (Yanai *et al*., 2006) because the fine roots are the principle pathway for nutrient absorption for plants (Eissenstat, 1992). Thus, studying the processes involving root dynamics is important in understanding forest functioning (Hendrick and Pregitzer, 1992), particularly in mangroves which invest proportionately large amounts of total productivity into root growth.

Understanding the belowground productivity under different mangrove densities will provide the opportunity to produce a complete picture about the total mangrove productivity, however the technical constraints have limited mangrove belowground studies to a few (e.g. Saintilan, 1997a,b; Komiyama *et al*., 2000; Alongi and Dixon, 2000; Ong *et al*., 2004; Comley and McGuinness, 2005; Tamooh *et al.*, 2008). Therefore the knowledge on belowground mangrove production is scanty (Tamooh *et al.*, 2008). The measured belowground biomass productions range between 0.72 to 30.62 kg m^{-2} worldwide (Komiyama *et al*., 2008; Tamooh *et al*., 2008) and the variations in floral diversity, tree density, forest age, the level of disturbances and tree growth rates have contributed to this large variance between different mangroves.

3.1.3 Rationale for the current study.

Mangrove plantings are carried out for habitat creation, protection against natural hazards such as tsunamis and to ensure a range of other ecosystem services such as carbon sequestration (Barbier, 2006; Field, 1998; Bosire *et al*., 2008). However, large-scale replanting schemes face huge technical obstacles and the information regarding planting techniques for mangrove species is still not adequate or complete (Siddiqi and Khan, 1996; Barbier, 2006). Particularly, due to unavailability of information on how mangrove survival, growth and biomass production respond to planting density, mangrove replanting activities are carried out at varying densities and hence this may contribute to varying successes with wasted resources. This implies the need to find the optimum planting density that results in the maximum survival, growth and biomass production over time.

The uncertainty about survival and growth under high mangrove densities has delayed applying high density plantations for increasing sediment accretion and soil elevation processes against the rising sea-level (Kumara *et al*. 2010). Absence of details on the planting density that yields the maximum total biomass production (belowground + aboveground) is also a serious limitation for mangrove planting activities if they are aimed at enhancing the absorption of CO_2. Unavailability of details on sediment nutrient (particularly N and P) dynamics in relation to changing mangrove tree density has also discouraged attaining the benefits of high dense mangrove plantations.

A properly controlled mangrove density experiment that allows the measurement of survival, growth, biomass production and nutrient dynamics under a range of densities and along a time series would fill these study gaps and conducting such a research was the prime objective of the current study. Furthermore, no studies on mangrove belowground productivity have been conducted in Sri Lanka and therefore the findings of this study will also be useful for local management purposes.

3.1.4 Aims and Objectives of the current study

No properly controlled experimental study has been published on the effects of mangrove plantation density on growth, survival, biomass productions, and sediment N and P dynamics. Therefore the aims of the current study are:

1) Studying the survival and the growth of mangroves under different planting densities and then reviewing the best density for optimum mangrove growth. The outcomes of this study will be useful in guiding mangrove replanting activities to create healthy mangrove stands faster and hence help the efficient utilization of resources, especially the available limited space.

2) Measuring the aboveground biomass production under different mangrove densities. This would review the optimum mangrove density for the highest aboveground biomass production. This will help accelerating the absorption of atmospheric CO_2 in future mangrove plantations through manipulation of the planting density.

3) Understanding the response of the belowground biomass production under different planting densities, both in terms of the number and the dry weight of the three different root types (coarse, medium and fine). The results of this study should be

useful in estimating the total biomass production (aboveground + belowground) under different mangrove densities.

4) Identifying the dynamics of sediment N and P under different mangrove densities. This study will review how the nutrient content in the sediment pool changes in relation to the changing tree density.

The objectives of the study were:

1) Conducting a three year long mangrove density experiment with sufficient numbers of treatments, and replicating the experiment at two different sites.

2) Collection of survival, growth and biomass data periodically.

3) Recording the changes of sediment N and P under different planting densities

4) Analysis of data for comparing the survival, growth and biomass production between the treatments and the sites.

3.1.5 Null and alternative hypothesis for the current study

The following hypothesis was tested under this part of the study.

Null hypothesis: The survival, growth, aboveground biomass, belowground biomass and soil nutrient levels are independent from mangrove density

Alternative hypothesis: The survival, growth, aboveground biomass, belowground biomass and soil nutrient levels depend on mangrove density

3.2 Materials and methods

3.2.1 Study sites and experimental design

The same *Rhizophora mucronata* plots prepared in four different densities (6.96, 3.26, 1.93 and 0.95 *R. mucronata* seedlings m^{-2}) for the sedimentation study (chapter 2) at Palakuda, in Puttalam lagoon, Sri Lanka were also used for this study. The experiment was also replicated in Rekawa lagoon (240ha / 6^0 05N and 80^0 50E), situated in Southern Sri Lanka. The lagoon lies in the intermediate climate zone receiving an annual rainfall between 1270-1910mm. The average temperature in the area ranges between 26.6 to 27.2 °C (Ganewatte *et al*., 1995; IUCN Sri Lanka, 2004). The lagoon receives freshwater from watersheds of Kirama Oya, Rekawa Oya and Urubokka Oya (Atapattu and Nissanka, 2005). Twenty 3.6-m × 3.6-m plots, arranged in four blocks of five treatments each, with a minimum gap of 1.2-m between plots, were demarcated in May 2007. Plots were randomly assigned to one of five treatments within each block, which included four planting densities (6.96, 3.26, 1.93 and 0.95 *R. mucronata* seedlings m^{-2}) and an unplanted control (0 seedlings m^{-2}). Planting densities equated to 100, 50, 36, 16 and 0 seedlings per treatment. Hence, each treatment was replicated four times within a randomized block design (figure 3.2).

Figure: 3.1. Location of the site within Rekawa Lagoon in Sri Lanka where the experimental plots were established (Source: Google Earth™ (2006) mapping service images)

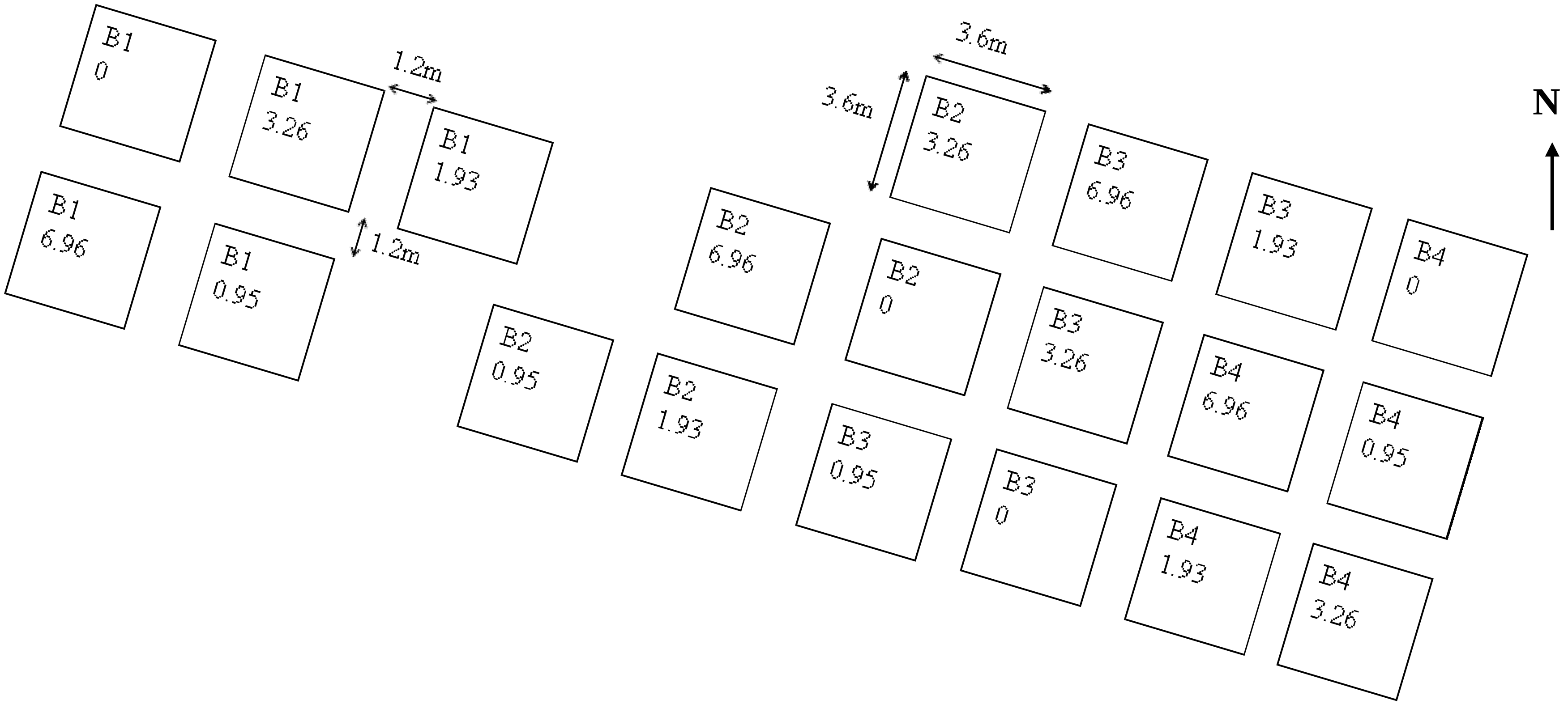

Figure:3.2 Experimental plot layout of different densities of *R. mucronata* seedlings planted in Rekawa Lagoon, Sri Lanka. (B1 to B4=experimental blocks; 6.96 to 0 indicates the planting densities of trees m^{-2}).

a

b

Figure:3.3 Rekawa experimental site, Rekawa Lagoon, Sri Lanka. (a- Planting of *R. mucronata* seedlings in 2007, b- the tree growth in plots by 2009).

3.2.2 Growth performances

3.2.2.1 Tree survival and Growth

Three sets of data were collected in June 2007, April 2008 and August 2009 from the Palakuda site, while a single set of data were taken in April 2009 from Rekawa. Thus, the samplings from Palakuda were carried out 400, 702 and 1171 days after planting. The Rekawa data set was recorded 702 days after planting so that it is more comparable with the second data set of Palakuda. All surviving seedlings were counted in all plots, and 20% of all trees per plot at Palakuda and 50% of all trees per plot at Rekawa were randomly selected for further measurement of height, diameter (at 50 cm height to clear the top of the propagule), number of branches, number of leaves and number of prop roots. The length and width of selected leaves were measured for every sampled plant and the leaf area was determined by copying the leaves on to grid papers. A leaf area vs. leaf length regression equation was generated from 21 *R. mucronata* leaves among different size classes collected from wild plants and this equation was used to determine the total leaf area of each plant using its mean leaf length and the total number of leaves.

3.2.2.2 Aboveground Biomass

Aboveground biomass for trees in each treatment was determined similarly to leaf area by developing a regression equation (plant height vs. dry matter weight) using 23 *R. mucronata* plants of different sizes collected from the wild. To generate this equation, all aboveground parts were removed and dried to a constant weight at 60°C.

Thereby the total aboveground dry weight for each treatment was calculated using the mean tree height, then summed by the number of plants for each treatment.

3.2.2.3 Belowground Biomass

A total of 48 soil cores (40-cm deep and 15-cm diameter) were taken as four sub samples from each planted plot density at Palakuda, Puttalam site after 1370 days of planting. Each core was sequentially cut in to 8 equal slices using a sharp knife. Each slice was washed over a 1-mm mesh and the extracted roots were sorted in to three classes; <5-mm diameter (fine roots), 5-10- mm (medium roots), and >10-mm (coarse roots). The three root types of each core were weighed to the nearest 0.01mg to record the wet weights of different root types per core. The roots were then dried to a constant weight at 60°C and were used for calculating the mean dry weight of fine, medium and coarse roots per core.

3.2.3 Sediment Nutrients

After 880 days (or approx. 2.4 years) after plantation establishment (Palakuda site), four sediment surface scrapes (1-cm depth × 10 x10-cm area) were taken from random points within each quarter of every plot and were combined to give one sample per plot. Samples were then dried and were exported to the Environmental engineering Research Center, Queen`s University of Belfast (UK). At the laboratory, the sediment samples were completely dried in an electric oven at 60°C and they were ground to fine powder using a Wiley mill. The samples were then subsampled for separate N, and P analysis. The nitrogen concentration (%) and the phosphate (%) in sediment samples were analyzed using Infra-Red Mass Spectrometry (IRMS) and SP6-350 Visible Spectrophotometer respectively.

3.2.4 Statistical Analysis

Data were examined for normality and homoscedasticity of residual variances. The % survival, aboveground dry mass (m^{-2}), the growth parameters (mean per tree values of height, stem diameter, numbers of branches, leaves and prop roots, leaf area), percentage sediment nitrogen and phosphate were compared using two-way ANOVA tests, with blocks and treatments as factors. All the four cores of each plot were averaged to find the mean values (m^{-2}) of fine, medium and coarse roots and they were compared between the treatments using two-way ANOVA (with blocks and treatments as factors) tests. Two-way ANOVA (with treatments and soil layers as factors and the fine roots density as the response) was used to compare the mean fine roots densities (m^{-2}) across the soil layers. The total belowground biomass ($g\ m^{-2}$) were compared between the densities using two-way ANOVA (with blocks and treatments as factors) test. Post-hoc tests were carried out where significant differences were found.

All the statistical analyses were carried out with Minitab, Version 14.20 (Minitab Inc., State College, PA, USA) or SPSS, Version 13.0 (SPSS Inc., Chicago, IL, USA) statistical packages.

3.3 Results

3.3.1 Leaf Area and Aboveground dry matter weight indices

3.3.1.1 Leaf Area index

The regression analysis of leaf area versus leaf length showed a strong fit (figure 3.4 and table 3.1) and hence the allometric equation of:

Leaf area (cm^{-2}) = - 47.6 + 8.13 Leaf Length was constructed for further calculations.

3.3.1.2 Aboveground dry matter weight index

The dry matter weight (g) and the height of plants collected from the wild showed a strong fit (figure 3.5 and table 3.2). Hence the allometric equation of: Dry matter weight (g) = - 653 + 20.4 Tree Height (cm) was constructed for further comparisons.

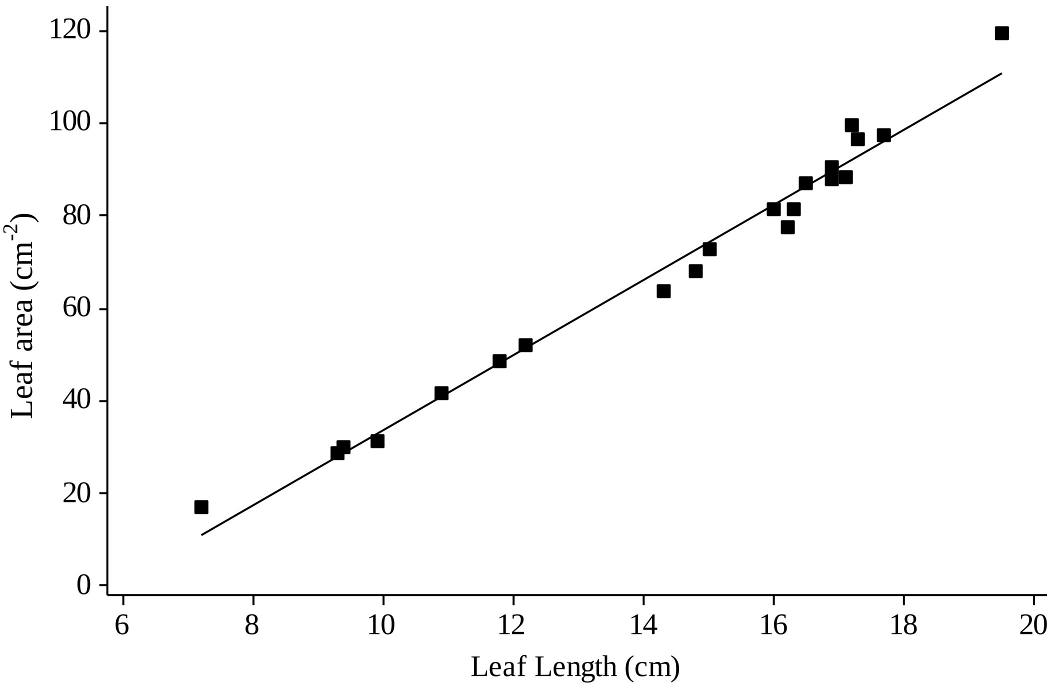

Figure: 3.4 Regression Analysis: leaf area versus leaf length of *R. mucronata*

Table: 3.1.Regression analysis between the leaf area and the leaf length of *R. mucronata* wild leaves collected form Puttalam Lagoon, Sri Lanka.

Predictor	Coefficient	SE of coefficient	T	P value
Constant	-47.60	3.88	-12.27	0.001
Length	8.13	0.26	31.00	0.001

S = 4.01 R-Sq= 98.12% r-Sq (adj) = 98.01%

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	15501	15501	960.78	0.001
Residual Error	19	307	16		
Total	20	15808			

Leaf area (cm^{-2}) = - 47.6 + 8.13 Leaf Length (cm)

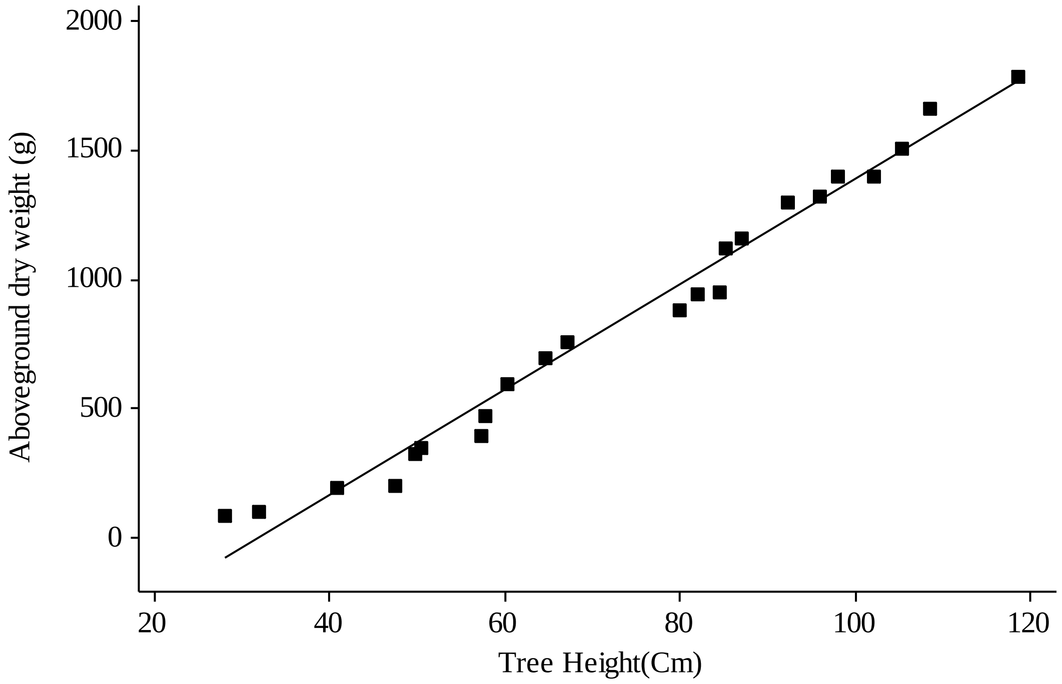

Figure: 3.5. Regression Analysis: aboveground dry matter weight versus plant height of *R. mucronata*

Table: 3.2. Regression analysis between dry matter weight and plant height of *R. mucronata* individuals collected form Puttalam Lagoon, Sri Lanka

Predictor	Coefficient	SE of coefficient	T	P value
Constant	-653.26	49.55	-13.18	0.001
Length	20.42	0.63	32.08	0.001

S = 76.72 R-Sq=98.01% r-Sq (adj) = 97.95%

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	6058881	6058881	1029.22	0.001
Residual Error	21	123625	5887		
Total	22	6182505			

Dry matter weight (g) = - 653 + 20.4 Tree Height(cm)

3.3.2 Growth performances

3.3.2.1 Palakuda, Puttalam Lagoon Site

3.3.2.1.1 Tree Survival

For Palakuda site, the mean survival rates (% ± S.E.) of trees after 1171 days were 93.4 (± 1.1), 84.2 (± 1.9), 85.7 (± 2.9), and 52.9 (± 6.0) for the 6.96, 3.26, 1.93, and 0.95 seedlings m^{-2} treatments, respectively. They showed significant differences among densities (Table 3.3) but not among blocks. Tukey`s comparisons showed that the lowest plantation density of 0.95 seedlings m^{-2}, had significantly lower survival than the other treatments (Figure 3.6 and Table 3.3).

Table: 3.3. Two-way ANOVA for mean % survival rates of different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1171 days of planting

Source of variance	DF	SS	MES	F value	P value
Treatment	3	2878.51	959.50	19.14	0.002
Block	2	4.56	2.28	0.05	0.956
Error	6	300.75	50.12		
Total	11	3183.82			

S = 7.08; R-Sq = 90.55%; R-Sq(adj) = 82.68%

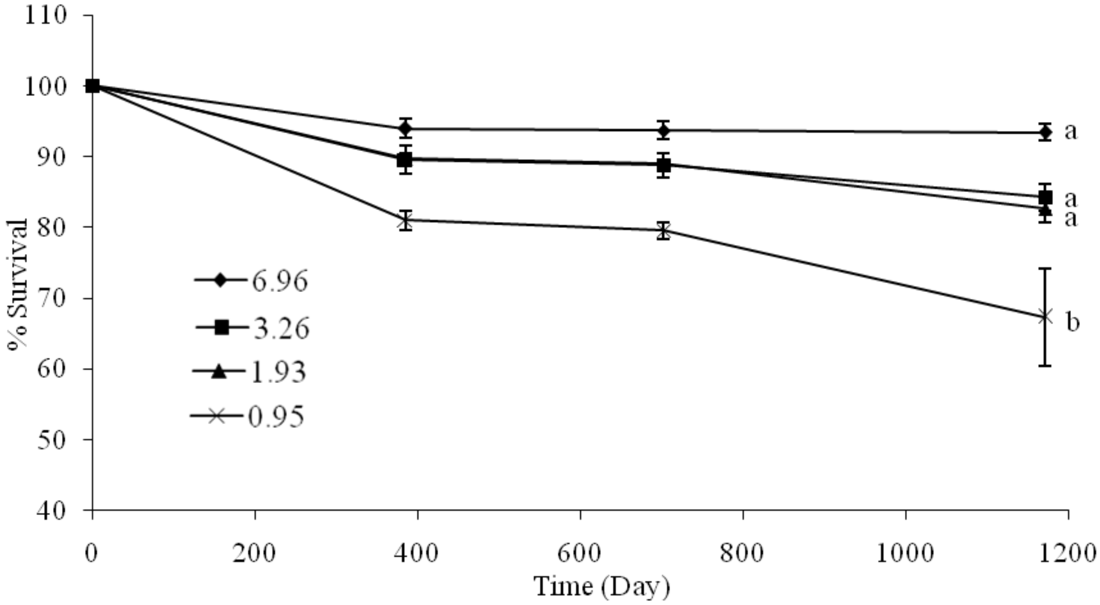

Figure: 3.6 Mean survivals (% ± S.E.) of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Lines represented by different letters identify significantly different mean annual survival rates at $\alpha = 0.05$. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}.

3.3.2.1.2 Tree Growth

No significant treatment effects were found ($p>0.05$) for the mean per tree values of the tree height, tree diameter, number of branches, number of leaves, number of prop roots, or leaf area after 1171 days (Table 3.4 and 3.5)

Table: 3.4. Mean (± SE) tree height, tree diameter, branches, leaves, roots and leaf area per plant at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1171 days of planting

Treatment (seedlings m^{-2})	Height (cm)	Diameter (cm)	No. of Branches	No. of Leaves	No. of Prop-Roots	Leaf Area (cm^2)
6.96	113.1 ±4.2	2.5 ± 0.5	7.2 ±0.5	72.9±6.2	8.4 ±1.0	1639.4±1.0
3.26	109.5 ±2.3	2.0 ±0.1	6.8 ±0.7	62.2±6.8	7.7 ±0.5	1507.6 ±1.4
1.93	112.3 ±6.5	2.0 ±0.1	7.4 ±0.4	65.8±2.4	8.6 ±0.3	1385.0 ±1.9
0.95	110.4 ±5.3	2.0 ±0.1	8.8 ±0.7	78.2±4.1	7.7 ±1.0	1856.8 ±0.9

3.3.2.1.3 Sediment Nitrogen and Phosphate

Sediment %N concentrations varied significantly among plantation densities (Table 3.6). The mean (± S.E.) percentage total sediment nitrogen values in the 6.96, 3.26, 1.93, 0.95 and 0 seedlings m^{-2} treatments were 0.076 (± 0.007), 0.066 (± 0.008), 0.068 (± 0.006), 0.069 (± 0.007) and 0.051 (± 0.001), respectively. The percentage total sediment nitrogen showed a significant decrease from the highest to the lowest plantation densities evaluated. According to the post-hoc tests, the % sediment N in 6.96 m^{-2} density was significantly higher over the all other densities while the densities of 3.26, 1.93, and 0.95 seedlings m^{-2} harboured similar sediment nitrogen concentrations. Sediments in the highest density treatment had 33.1% greater sediment N compared to the controls whilst other densities had only 22.9% to 26.6% greater sediment N than the controls. The %phosphate concentration in sediment was not significantly different between densities ($p>0.05$; Table 3.7). The mean (± S.E.) %phosphate concentration values in the 6.96, 3.26, 1.93, 0.95 and 0 seedlings m^{-2} treatments were 0.017 (± 0.002), 0.027 (± 0.005), 0.011 (± 0.006), 0.018 (±0.004) and 0.015 (± 0.003) respectively.

Table: 3.5. Two-way ANOVA for growth parameters (per plant) of different *R. mucronata* density treatments planted in Puttalam Lagoon; after 1171 days of planting

	Source of variance	DF	SS	MES	F value	P value
Tree height	Treatment	3	24.96	8.32	0.10	0.958
	Block	2	50.89	25.44	0.30	0.751
	Error	6	506.95	84.49		
	Total	11	582.84			
	S = 9.19; R-Sq = 13.02%; R-Sq(adj) = 0.00%					
Tree diameter	Treatment	3	0.57	0.19	6.74	0.564
	Block	2	0.35	0.17	0.68	0.542
	Error	6	1.54	0.26		
	Total	11	2.45			
	S = 0.51; R-Sq = 37.44%; R-Sq(adj)=0.00%					
No. of branches	Treatment	3	6.62	2.20	1.85	0.238
	Block	2	2.17	1.08	0.91	0.443
	Error	6	7.15	1.19		
	Total	11	15.94			
	S =1.09; R-Sq =55.17%; R-Sq(adj) =17.82%					
No. of leaves	Treatment	3	1723.51	574.50	6.89	0.231
	Block	2	155.79	77.89	0.93	0.443
	Error	6	500.44	83.41		
	Total	11	2379.73			
	S = 9.13; R-Sq = 78.97%; R-Sq(adj) =16.45%					
No. of prop roots	Treatment	3	1.97	0.66	0.54	0.670
	Block	2	6.27	3.14	2.60	0.154
	Error	6	7.25	1.21		
	Total	11	15.50			
	S = 1.099; R-Sq = 53.22%; R-Sq(adj) = 14.23%					
Leaf area	Treatment	3	252212	84071	0.47	0.716
	Block	2	424770	212385	1.18	0.370
	Error	6	1079761	179960		
	Total	11	1756744			
	S = 424.21; R-Sq = 38.54% ; R-Sq(adj) = 0.00%					

Table: 3.6. Two-way ANOVA for mean % sediment nitrogen of different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 880 days of planting.

Source of variance	DF	SS	MES	F value	p value
Treatment	4	0.03	0.02	4.37	0.036
Block	2	0.02	0.01	6.19	0.024
Error	8	0.01	0.01		
Total	14	0.05			

S = 0.01; R-Sq = 78.87%; R-Sq(adj) = 63.02%

Table: 3.7 Two-way ANOVA for sediment %Phosphate of different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka after 880 days

Source of variance	DF	SS	MES	F value	p value
Treatment	4	0.04	0.01	0.04	0.060
Block	2	0.09	0.05	0.01	0.269
Error	8	0.02	0.03		
Total	14	0.07			

S = 0.02; R-Sq =26.14%; R-Sq(adj) = 38.60%

3.3.2.2 Rekawa Site

3.3.2.2.1 Tree Survival

For Rekawa site, mean survival rates (% ± S.E.) of trees after 702 days were 91.25 (± 1.38), 80.0 (± 2.16), 76.75 (± 0.85), and 74.0 (± 1.96) for the 6.96, 3.26, 1.93, and 0.95 seedlings m^{-2} treatments, respectively. The values showed significant differences between treatments (Table 3.8) but not between blocks. Tukey`s comparisons showed that the highest plantation density, of 6.96 seedlings m^{-2}, had significantly higher survival than the other treatments.

Table: 3.8. Two-way ANOVA for % tree survival at different density treatments of *R. mucronata* seedlings planted in Rekawa Lagoon, Sri Lanka; after 702 days of planting.

Source of variance	DF	SS	MES	F value	P value
Treatment	3	160.77	53.59	1.78	0.022
Block	3	341.56	113.85	3.77	0.053
Error	9	271.63	30.18		
Total	11	773.97			

S = 5.49; R-Sq = 64.90%; R-Sq(adj) = 41.51%

3.3.2.2.2 Tree Growth

No significant treatment effects were found ($p>0.05$) for the mean per tree values of the tree height, tree diameter, number of branches, number of leaves, number of prop roots, or leaf area after 702 days of planting (Table 3.9 and 3.10).

Table: 3.9. Mean (± SE) tree height, tree diameter, branches, leaves, roots and leaf area per plant at different density treatments of *R. mucronata* seedlings planted in Rekawa Lagoon, Sri Lanka; after 702 days of planting.

Treatment (seedlings m^{-2})	Height (cm)	Diameter (cm)	No. of branches	No. of Leaves	No. of prop Roots	Leaf area (cm^2)
6.96	94.9±1.1	1.5±0.1	3.7±0.2	35.1±1.6	2.4±0.4	1294.5±4.2
3.26	93.3±2.6	1.3±0.1	3.3±0.3	28.5±3.9	1.9±0.4	967.5±11.4
1.93	91.9±3.4	1.3±0.0	2.9±0.3	25.4±2.0	1.6±0.3	912.6±17.9
0.95	95.3±1.8	1.5±0.1	3.7±0.3	39.2±5.8	2.2±0.2	1329.5±12.9

Table: 3.10. Two-way ANOVA for growth parameters (per plant) at different density treatments of *R. mucronata* seedlings planted in Rekawa Lagoon, Sri Lanka; after 702 days of planting

	Source of variance	DF	SS	MES	F value	P value
Tree height	Treatment	3	29.79	9.93	0.51	0.682
	Block	3	107.43	35.81	1.86	0.207
	Error	9	173.581	19.29		
	Total	15	310.794			
	S = 4.39; R-Sq = 44.15% ; R-Sq(adj) = 6.92%					
Tree diameter	Treatment	3	0.24	0.08	2.50	0.126
	Block	3	0.01	0.00	0.10	0.960
	Error	9	0.28	0.03		
	Total	15	0.53			
	S = 0.178; R-Sq = 46.36%; R-Sq(adj) = 10.61%					
No. of branches	Treatment	3	1.90	0.64	1.62	0.234
	Block	3	1.71	0.57	1.28	0.327
	Error	9	2.81	0.31		
	Total	15	6.44			
	S = 0.56; R-Sq = 56.24%; R-Sq(adj) = 27.07%					
No. of leaves	Treatment	3	469.86	156.62	2.40	0.135
	Block	3	101.44	33.81	0.52	0.680
	Error	9	586.22	65.13		
	Total	15	1157.53			
	S = 8.07; R-Sq = 49.36% ; R-Sq(adj) =15.59%					
No. of prop roots	Treatment	3	1.32	0.44	1.07	0.410
	Block	3	1.23	0.41	1.00	0.437
	Error	9	3.72	0.41		
	Total	15	6.27			
	S = 0.64; R-Sq = 40.77% ; R-Sq(adj) = 1.28%					
Leaf area	Treatment	3	5.62	187266493	2.14	0.139
	Block	3	1.67	556266694	0.28	0.835
	Error	9	6.39	710636723		
	Total	15	1.37			
	S = 26658; R-Sq = 53.26% ; R-Sq(adj) = 22.09%					

3.3.2.3 Comparison of Rekawa and Palakuda data

Table: 3.11. Mean % survival (± SE) at different density treatments of *R. mucronata* seedlings planted in Puttalam and Rekawa Lagoons, Sri Lanka; after 702 days of planting.

Treatment (Seedlings m^{-2})	%Survival In Puttalam Lagoon	%Survival In Rekawa Lagoon
6.96	93.7 ± 1.2	91.2 ± 1.4
3.26	88.8 ± 1.7	80.0 ± 2.2
1.93	89.0 ± 0.5	76.7 ± 0.8
0.95	79.6 ± 1.2	74.0 ± 1.9

Table: 3.12. Mean (± SE) tree height, tree diameter, branches, leaves, prop roots and leaf area per plant at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 702 days of planting.

Treatment (seedlings m^{-2})	Height (cm)	Diameter (cm)	No. of branches	No. of Leaves	No. of prop Roots	Leaf area (cm^2)
6.96	99.8±3.7	1.6±0.0	5.8±0.4	50.7±5.3	7.4±1.3	1237.4±53.1
3.26	90.9±1.0	1.4±0.0	4.3±0.4	35.7±4.7	4.2±0.7	1008.8±59.1
1.93	93.34±1.5	1.6±0.2	5.2±0.8	41.5±6.8	6.1 ±1.8	1044.8±51.9
0.95	90.1±2.3	1.4±0.1	5.2±0.6	36.4±5.3	4.6±1.0	1142.7±15.1

The tallest trees (99.8 ± 3.7) were recorded from the 6.96 density of Palakuda plots whilst the 3.26 and 0.95 Rekawa densities showed taller trees than their counterparts in Palakuda. The largest diameter (1.6 ± 0.1), highest numbers of branches (5.8 ± 0.4), leaves (50.7 ± 5.3) and prop roots(7.4 ± 1.3) have been recorded from the Palakuda plots while the largest leaf area (1329.5 ± 12.9) was from Rekawa plots (Table 3.9 and 3.12).

3.3.3 Biomass Production

This section containes both aboveground and belowground biomass studies at Palakuda, Puttalam site and the aboveground biomass study at Rekawa site.

3.3.3.1 Aboveground Biomass Production

3.3.3.1.1 Palakuda, Puttalam Lagoon

The aboveground biomass per unit area (m^{-2}) responded significantly to plantation density (Table 3.13), with higher plantation densities equating to greater biomass. While the individual tree size did not differ among treatments (Table 3.5), greater numbers of seedlings in high density plots combined with high survival rates (Figure 3.6), interacted to promote consistently greater biomass per unit of ground area as plantation densities increased over the duration of the experiment, and not just at the very end of the experiment (Figure 3.7).

Table: 3.13. Two-way ANOVA for mean aboveground biomass (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1171 days of planting

Source of variance	DF	SS	MES	F value	P Value
Treatment	3	163897467	546324489	121.20	0.001
Block	2	1074840	537420	1.19	0.366
Error	6	2704674	450779		
Total	11	167676980			

S = 671.42; R-Sq = 98.39%; R-Sq(adj) = 97.04%

Table: 3.14. Mean (± SE) aboveground biomass (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1171 days of planting.

Density (Seedlings m^{-2})	Aboveground biomass (g dry weight m^{-2})
6.96	10772 ± 24
3.26	4344 ± 12.1
1.93	2638 ± 10.1
0.95	1041 ± 8.3

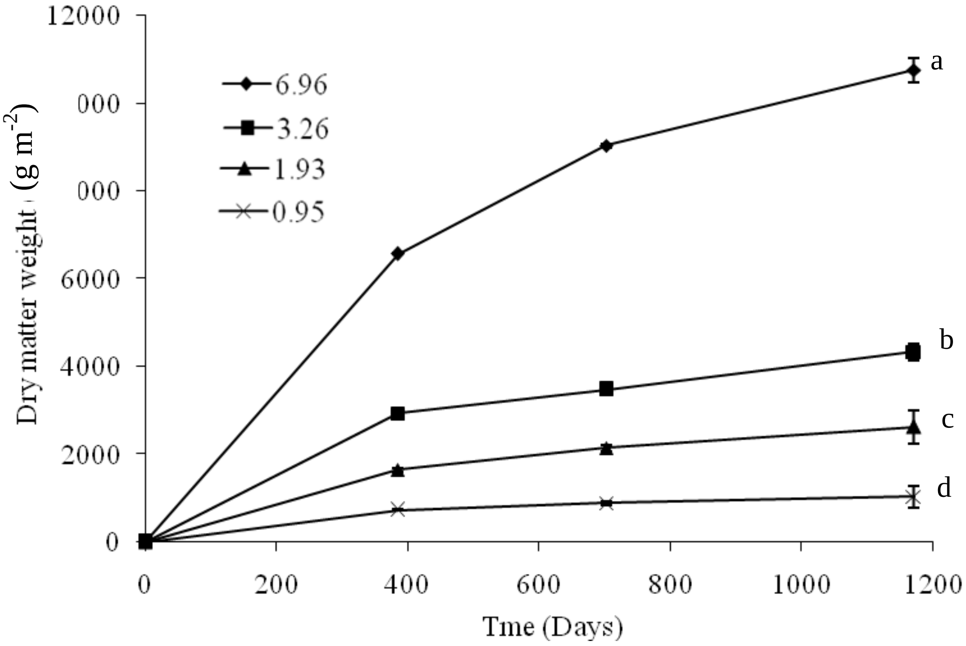

Figure: 3.7. Mean (± S.E.) aboveground biomass accumulation (g m^{-2})at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Lines represented by different letters identify significantly different mean annual biomass accumulation rates at $\alpha = 0.05$. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

3.3.3.1.2 Rekawa Site

The aboveground biomass per unit area (m^{-2}) responded significantly to plantation density after 702 days (Table 3.15), with higher plantation densities equating to greater biomass (Table 3.16).

Table: 3.15. Two-way ANOVA for mean aboveground biomass (gm^{-2}) at different density treatments of *R. mucronata* seedlings planted in Rekawa Lagoon Sri Lanka; after 702 days of planting

Source of variance	DF	SS	MES	F value	p value
Treatment	3	171105537	57035179	536.95	0.001
Block	3	565604	188535	1.77	0.222
Error	9	955982	106220		
Total	15	172627123			
S = 325.93; R-Sq = 99.45%; R-Sq(adj) = 99.08%					

Table: 3.16. Mean (± SE) aboveground biomass (gm^{-2}) at different density treatments of *R. mucronata* seedlings planted in Rekawa Lagoon, Sri Lanka; after 702 days of planting.

Density (Seedlings m^{-2})	Aboveground biomass (g dry weight m^{-2})
6.96	9904 ± 18.1
3.26	4828 ± 22.1
1.93	3396 ± 20.1
0.95	1596 ± 38.3

3.3.3.2 Belowground Biomass

3.3.3.2.1 Density of different root types (m^{-2})

The mean number of fine roots m^{-2} and the total roots m^{-2} showed significant difference between the densities (tables 3.17 and 3.18). Tukey`s comparisons showed that the highest tree density (6.96) contains the highest fine and total root densities (m^{-2}) over the lowest density (0.95). The fine root density was not significantly different ($p>0.05$) between the other densities. None of the densities showed significant differences ($p<0.05$) for medium or coarse roots (Figure 3.8).

Table: 3.17. Mean number (± SE) of different root types (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting

Density (Seedlings m^{-2})	Mean number of roots (m^{-2})			
	Fine	Medium	Coarse	Total
6.96	3751 ± 426	159.1 ± 58.8	173.2 ± 50.3	4083 ± 536
3.26	2157 ± 588	38.9 ± 15.4	88.4 ± 33.6	2284 ± 635
1.93	1885.5 ± 84.3	54.2 ± 31.2	68.4 ± 25.8	2008.1 ± 96.6
0.95	1574 ± 359	36.5 ± 10.5	45.96 ± 2.04	1657 ± 362

Table: 3.18. Two-way ANOVA for the density of different root types (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting a=Fine roots b=Medium roots c=Coarse roots d= Total roots

a

Source of variance	DF	SS	MES	F value	P value
Treatment	3	8451780	2817260	7.65	0.021
Block	2	1772432	886216	2.41	0.173
Error	6	2209659	368277		
Total	11	1243872			
S = 606.92; R-Sq = 82.23%; r-Sq (adj) = 67.42%					

b

Source of variance	DF	SS	MES	F value	P value
Treatment	3	30765.92	10255.34	3.17	0.081
Block	2	12089.50	6044.83	2.18	0.192
Error	6	16600.51	2766.81		
Total	11	59455.93			
S = 52.60; R-Sq = 72.08%; r-Sq (adj) = 48.81%					

c

Source of variance	DF	SS	MES	F value	P value
Treatment	3	27826.71	9275.55	2.35	0.173
Block	2	2264.21	1132.12	0.29	0.762
Error	6	23718.73	3953.12		
Total	11	53809.62			
S = 62.87 ; R-Sq = 55.92%; r-Sq (adj) = 19.19%					

d

Source of variance	DF	SS	MES	F value	P value
Treatment	3	10574406	3524802	7.61	0.018
Block	2	2206300	1103150	2.38	0.173
Error	6	2779678	463280		
Total	11	15560383			
S = 680.62; R-Sq = 82.14%; r-Sq (adj) = 67.25%					

3.3.3.2.2 Fine root density (m^{-2}) in different soil depths

According to the Two-way ANOVA test, in the 5-10cm layer (L2), the mean fine roots density m^{-2} (Table 3.19) significantly varied between the densities. According to Tukey`s comparisons, the mean fine roots density of the 6.96 density (805 ± 121 m^{-2}) was significantly higher ($p<0.05$) than those of the 1.93 (281.6 ± 11.6) and 0.95 (333.5 ± 83.4) densities while the 3.26 density did not differ from the 6.96. The 3.26, 1.93 and 0.95 densities were not different from each other within this 5-10cm layer. The mean fine roots density (m^{-2}) of different densities significantly differed in the 10-15cm layer (L3) where the 6.96 density (753 ± 90.4 m^{-2}) was significantly higher

($p<0.05$) than those of the 0.95 (321.7 ± 50.5). All the other densities were not different from each other or from 6.96 density (Appendix 1). All the densities showed a general pattern of reducing their fine root densities with the depth (figure 3.9).

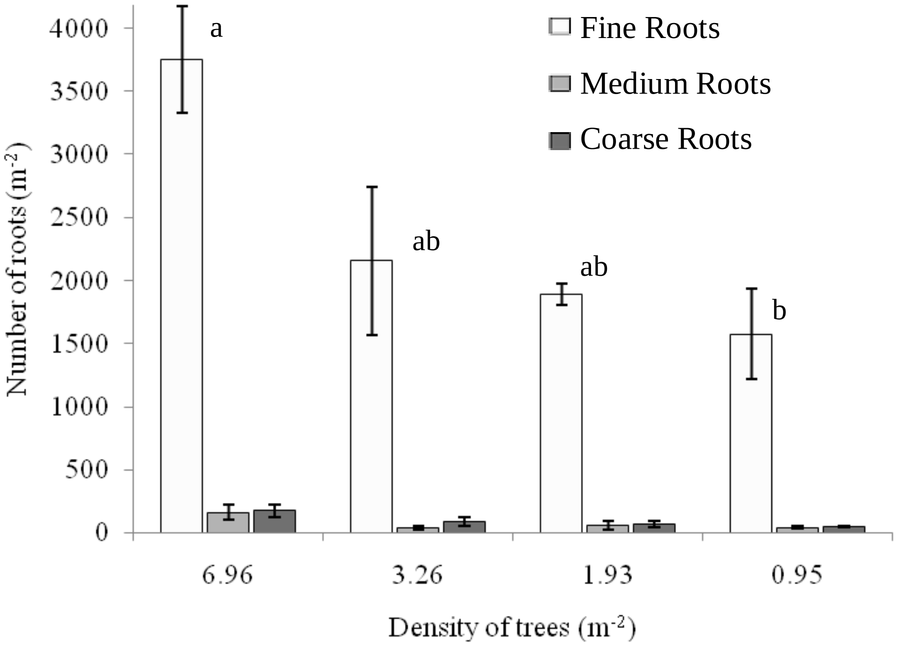

Figure 3.8 Mean number of different roots (± S.E.) of *R. mucronata* seedlings at different densities of *R. mucronata* seedlings planted in Palakuda, Puttalam Lagoon after 1370 days. Columns represented by different letters identify significantly different mean number of different roots at $\alpha = 0.05$.

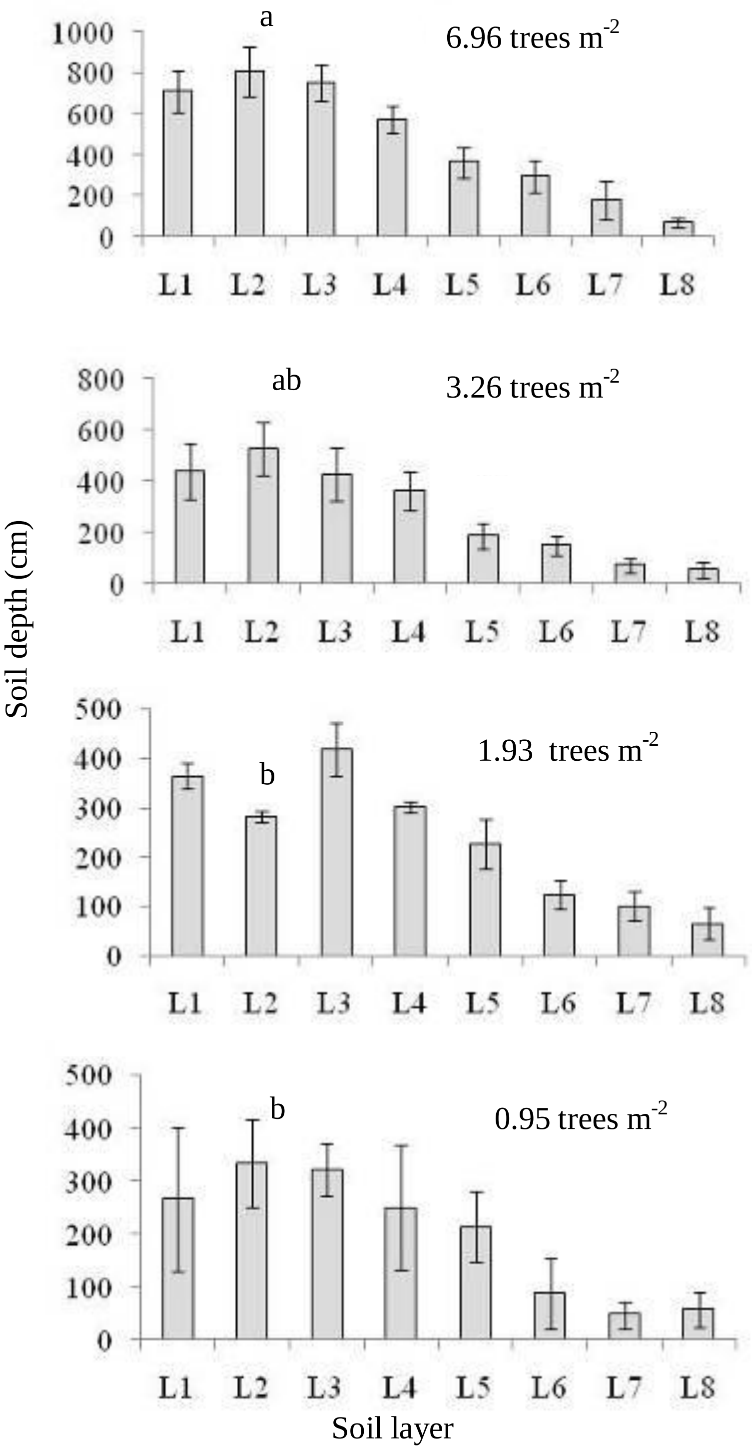

Figure: 3.9 Distribution of fine roots (Mean ± SE) in different soil depths under different density treatments of *R. mucronata* seedlings; Puttalam Lagoon, Sri Lanka; after 1370 days of planting. L1=0-5cm, L2=5-10cm, L3=10-15cm, L4=15-20cm, L5=20-25cm, L6=25-30cm, L7=30-35cm, L8=35-40cm. Columns represented by different letters identify significantly different mean number of different roots at $\alpha = 0.05$.

Table: 3.19. Two-way ANOVA for the mean fine root densities (m^{-2}) within different soil layers of *R. mucronata* density treatments; Puttalam Lagoon, Sri Lanka, after 1370 days of planting.

L1=0-5cm, L2=5-10cm, L3=10-15cm, L4=15-20cm, L5=20-25cm, L6=25-30cm, L7=30-35cm, L8=35-40cm.

	Source of variance	DF	SS	MES	F value	P value
L1	Treatment	3	325261	108420	0.12	0.116
	Block	2	35985	17993	0.63	0.631
	Error	6	216052	36009		
	Total	11	577299			
	S = 189.82; R-Sq = 62.58%; R-Sq(adj) = 31.39%					
L2	Treatment	3	505082	168361	6.74	0.024
	Block	2	48160	24080	0.96	0.433
	Error	6	149820	24970		
	Total	11	703062			
	S = 158.01; R-Sq = 78.69%; R-Sq(adj) = 60.93%					
L3	Treatment	3	318380	106127	6.07	0.030
	Block	2	38698	19349	1.11	0.390
	Error	6	104946	17491		
	Total	11	462024			
	S = 132.31; R-Sq = 77.29%; R-Sq(adj) = 58.36%					
L4	Treatment	3	183071	61023.6	3.43	0.093
	Block	2	35031	17515.3	0.99	0.427
	Error	6	106662	17777		
	Total	11	324763			
	S = 133.32; R-Sq = 67.16%; R-Sq(adj) 39.79%					

Table 3.19 continue..

	Source of variance	DF	SS	MES	F value	P Value
L5	Treatment	3	57244	19081.42	4.59	0.054
	Block	2	66668	33334.11	8.02	0.020
	Error	6	24947	4157.93		
	Total	11	148860			
	S = 64.48; R-Sq = 83.24%; R-Sq(adj) = 69.28%					
L6	Treatment	3	76762	25587.31	8.57	0.014
	Block	2	600019	30009.42	10.06	0.012
	Error	6	17907	298.41		
	Total	11	154687			
	S = 54.63; R-Sq = 88.42% ; R-Sq(adj) = 78.78%					
			28984.51	9661.51	1.54	0.297
L7	Treatment	3	26999.32	13499.73	2.16	0.197
	Block	2	37552.43	6258.72		
	Error	6	93536.31			
	Total	11				
	S = 79.11; R-Sq = 59.85%; R-Sq(adj) = 26.40%					
L8	Treatment	3	358.31	119.43	0.06	0.980
	Block	2	8563.72	4281.85	1.06	0.208
	Error	6	12459.11	2076.52		
	Total	11	21381.23			
	S = 45.57; R-Sq = 41.73%; R-Sq(adj) = 0.00%					

3.3.3.2.3 Belowground dry weight

The total belowground biomass (g m^{-2}) significantly varied between the treatments (Table 3.20). Tukey`s comparisons showed that the highest tree density (6.96) contained the highest belowground dry weight (105.41 ± 6.98 g m^{-2}; Table 3.4) while the other densities did not significantly differ (p>0.05) from each other.

Table: 3.20. Two-way ANOVA for belowground dry weight (g m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting

Source of variance	DF	SS	MES	F value	P value
Treatment	3	11022.52	3674.16	9.79	0.012
Block	2	548.41	274.22	0.73	0.520
Error	6	2252	375.39		
Total	11	13823.31			
S = 19.38	R-Sq = 83.71%	r-Sq (adj) = 70.13%			

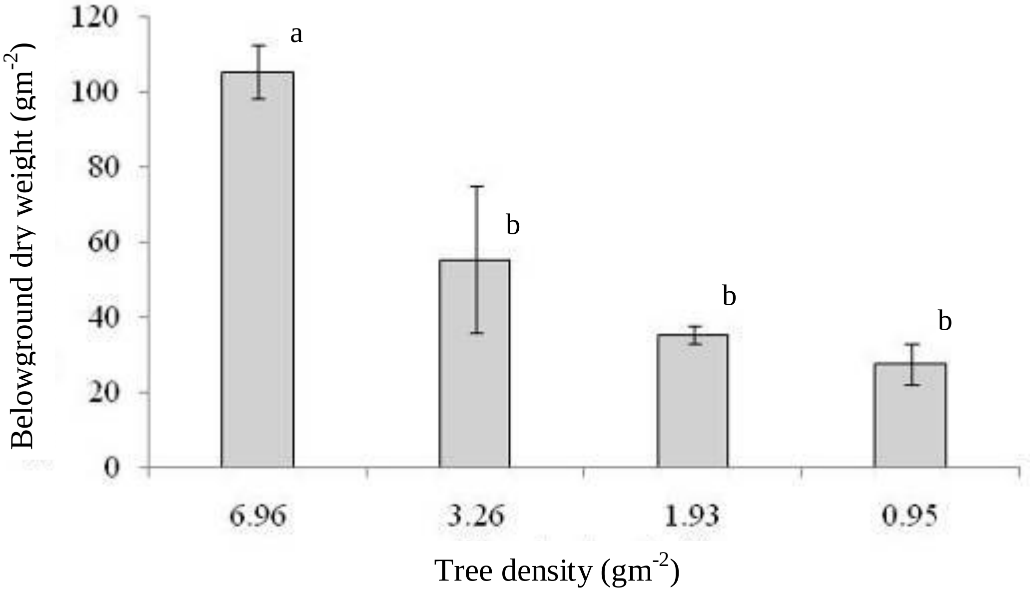

Figure: 3.10. Belowground dry weights (± S.E.) of *R. mucronata* seedlings at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting.

3.4 Discussion

3.4.1 Growth Performances

Facilitation has been defined as ‘positive, non-trophic interactions that occur between physiologically independent plants and that are mediated through changes in the abiotic environment or through other organisms’ (Brooker *et al.*, 2008). Such interactions are particularly common in stressed environments (Bertness and Leonard, 1997; Callaway, 2007; Brooker *et al.*, 2008). Since mangroves grow in the inter-tidal zone where plants can be stressed by tidal movements, excess salt and limited freshwater, it is a prime environment for documenting facilitation (Gedan and Silliman, 2009). Whilst such effects have been shown between mangroves and other species (e.g. McKee *et al.*, 2007) there are currently no published demonstrations of intraspecific facilitation by mangroves. The density experiment at Palakuda, Puttalam Lagoon site demonstrated that survival of *R. mucronata* plantings was enhanced at greater plantation densities (including densities of 6.96, 3.26, and 1.93 seedlings m^{-2}; Figure 3.6) compared to the lowest plantation density of 0.95 seedlings m^{-2}. In fact, differences in survival between the treatments were apparent at the first survey date and persisted (and widened) up until 1171 days. The cause of this positive density-dependence may be related to the enhanced sediment accretion at higher densities. As suggested here, sediment accretion has been shown to stimulate the growth of mangroves by increasing nutrient availability (de Olff *et al.*, 1997; Hemminga *et al.*, 1998; Alongi *et al.*, 2005; Lovelock *et al.*, 2007), a pattern consistent with the higher sediment nitrogen that was recorded in the high density treatments. Along with a decrease in sediment nitrogen concentrations from the most dense to least dense *R.*

mucronata seedling plantations, the physical support provided by tighter plantation densities also promotes survival, at least until plantations become stands and are subjected to self-thinning.

Phosphorus deficiency may limit growth and cause dwarf trees (Feller 1995). The absence of a growth reduction of the trees coupled with unchanged sediment phosphate levels in the higher densities at Palakuda suggests that phosphate is not limiting growth at this site; it is perhaps naturally rich in phosphate to maintain these high densities or the sediment accretion has just provided the difference between the demand and the supply. Since tidal inundation influences phosphate retention and release reactions, its concentration may vary with the sediment depth in mangroves (Ranjan *et al.*, 2009). However, the present study looked at the phosphorous of the surface sediment only and this experiment needs to be extended to a depth-wise analysis in order to find the total effect of the tree density on the soil phosphate levels.

Both Rekawa data and Palakuda second data set were recorded 702 days after planting and Rekawa showed similarities to the Palakuda site in terms of the tree survival and growth. The trees of the highest density (6.96 trees m^{-2}) resulted in the highest survival for both sites. This further confirms the positive impacts of increased tree density on survival during the early growth of mangroves, and demonstrates that the effect is not an idiosyncratic result of specific site conditions at Palakuda.

However the Palakuda treatments showed higher survival over the counterpart densities in Rekawa (Appendix 2). Frequent exchange of high tide and low tides have been identified as important factors for mangrove growth as the high tide brings nutrients while the ebb tide sweeps away the toxic components (e.g. Soil H_2S) that inhibit mangrove growth. The enhanced survival in Palakuda lagoon therefore could be associated with regular tidal variations which are not observed for Rekawa as its lagoon mouth is interrupted by sand formations for months during the year.

There were no significant differences in the various measures of individual tree growth among treatments over the course of study for both Palakuda and Rekawa sites. The absence of any growth differences in growth parameters (per tree values of; tree height, diameter, number of branches, number of leaves, number of prop roots or leaf area) between densities was observed for both sites demonstrating an apparent lack of negative effects of competition at high densities. Due to self-thinning in crowded mangroves (Analuddin *et al*., 2009) and density-dependent mangrove mortality (Proffitt and Devlin, 2005) documented as long-term processes in mangroves, a reduction in survival and growth can eventually be expected in higher densities in the future. There was certainly no evidence for competitive effects after 1171 days of growth; instead the absence of any differences in growth and the widening gap in survival rates suggests the continued importance of facilitation at these early stages of stand development.

3.4.2 Aboveground Biomass production

At Palakuda site, the highest mangrove density (6.96 seedlings m^{-2}) showed the greatest annual rate of above ground biomass accumulation for the period of 1171 days, suggesting that high density plantations may act as the most efficient sinks for atmospheric carbon during their early phase of growth. Planting mangroves at 6.96 seedlings m^{-2} increased the per-area biomass by 10 times compared with the 0.95 seedlings m^{-2} density. The greater aboveground biomasses in higher densities were also apparent for the 702 days growth in Rekawa site.

There was clearly no evidence yet of natural thinning, or even self-pruning, in the present experimental stands after 1171 days, rather the total biomass trajectories of the different treatments continue to diverge despite the high initial densities of seedlings in comparison to most natural stands. Hence, these results suggest that planting at high densities will result in better survival combined with higher biomass accumulation over at least the first three years.

3.4.3 Belowground Biomass production

The fine roots are more efficient in absorbing nutrients than the coarser ones as they dramatically increase the surface area for absorption. In the highest tree density, the nutrient demand from the soil should obviously be higher and therefore the trees of that density need a special strategy to accelerate the rates of nutrient absorption. The most successful way for this seems to be increasing the absorption surface through the increase of the fine root densitiy. In fact, this has been observed in the highest density with 3751 ± 426 m^{-2} fine roots which is 2.4 times higher than that of the lowest density (1574 ± 359). Thus, increasing the density by approximately 7.3 times has increased the fine root density by 2.4 time for overcoming the higher nutrient demand. The frequent wave and tidal activities are likely to disturb the nutrient absorption in the upper most 0-5cm layer and this could be the reason for less fine roots in this layer compared to the underneath 5-10cm region which is more stable from disturbances. The general trend of reducing the fine root density with the depth shown by all the other planting densities (Figure 3.9) also indicated the importance of the upper soil layers in nutrient absorption.

The reported world mangrove belowground production ranges between 0.72 to 30.62 kg dry matter m^{-2} (Komiyama *et al.*, 2008; Tamooh *et al.*, 2008) whilst the belowground biomass production in this study, even in the highest tree density (105.41 ± 6.98 g dry matter m^{-2}), did not reach even the lowest limit of this range. The literature range comprises mostly natural mangroves and occasionally older (>5years) planted mangroves in comparison to our 1370 day plants which have not developed their complete systems of roots yet.

The highest density (6.96 m^{-2}) contained the highest belowground dry weight (105.41 ± 6.98 g m^{-2}) compared with all the other densities, whilst this parameter did not differ between the other densities. Thus, the belowground dry weight did not increase proportionally with the increasing tree density as was the case with the aboveground biomass production. The reason for this is not obvious and uneven growth of roots in the intermediate densities (3.26, 1.93 and 0.95m^{-2}) could be the case with this however, it needs further research to understand the actual reasons for this un-proportionate growth.

3.5 Conclusions

Higher densities of planted mangroves at two different lagoons (Puttalam and Rekawa) recorded greater survival and there was no evidence that increasing plant density evoked a trade-off with growth and survival of the planted trees. Sediment %N was significantly different among densities which suggest one potential causal mechanism for the facilitatory effects observed: high densities of plants potentially contribute to the accretion of greater amounts of nutrient rich sediment. The highest density produced more fine roots in the upper soil layers presumably increasing nutrient absorption in response to the higher nutrient demand for the crowded trees. However, the N content and root data were not recorded over comparable depth horizons during the study. While these potential processes need further research, rather, facilitatory effects enhanced survival at high densities, suggesting that managers may be able to take advantage of high plantation densities to help fixating excess atmospheric carbon at least during the early 1171 days of mangrove development.

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CHAPTER 4- EFFECTS OF TREE DENSITY ON CHANGES OF MACROFAUNA IN PLANTED MANGROVES

4.1 Introduction

This section focuses on the changes of sediment macrofauna communities in relation to mangrove density in planted mangroves.

4.1.1 Mangrove Macrofauna

The particulate and dissolved organic materials in mangrove sediment provide food for various sediment invertebrates (Alongi, 1998). The mangrove vegetation structure contributes to habitat complexity and diversity of sediment fauna (Hutchings and Saenger, 1987; Lee, 1998) while the composition of mangrove sediment fauna may change depending on the sediment characteristics (Gray 1974; Kathiresan and Bingham, 2001), tidal inundation (Defeo and McLachlan, 2005) or habitat complexity and floral structure (Lindegarth and Hoskin, 2001).

The mangrove macrobenthos is composed of a number of phyla, including Porifera (sponges), Mollusca (molluscs), Arthropoda (crabs, lobsters, prawns, etc.), Annelida (segmented worms), Sipunculoidea (peanutworms), Platyhelminthes (flatworms), Tunicates and Ascidians (Ellison, 2008; Nagelkerken, *et al*. 2008; Cannicci, *et al*., 2008). The burrows of some mangrove soil animals (particularly crabs) transport salt, nutrients, oxygen and toxins when they are inundated by water. Some polychaetes stabilize the accreted sediments by secreting mucopolysaccharides that glue sediment particles together (Paterson *et al*., 1986; Raffaelli and Hawkins, 1996) and thus they would preserve the accreted mangrove sediments which are important sources of nutrients during early mangrove growth (Kumara *et al*., 2010). These benthic fauna are essential components of aquatic food webs as they are food for fish and invertebrates (Kathiresan and Bingham, 2001). The feeding behaviours of benthic crustaceans and molluscs on mangrove detritus provide energy for higher consumers in the food webs including birds and commercial fish species (Sasekumar, 1974; Jones, 1984). Grazing on vegetative structures and the burrowing habits of macrofauna also modify the physical and vegetation structure of mangroves (Berry, 1972; Smith, 1987; Smith *et al*., 1991). The macrofaunal diversity and abundance therefore may reflect the status and functioning of mangrove ecosystems and serve as potential biological/ecological indicators of habitat change in both natural and managed mangroves (Macintosh *et al*., 2002).

4.1.2 Studies on Mangrove Macrofauna in Sri Lanka

Macrofaunal studies in Sri Lanka are rare (Coastal Conservation Department Sri Lanka 2007) and there are no detailed studies of mangrove infauna from Sri Lanka. Pinto (1986) described 11 crab species, 4 gastropods, and 4 bivalves from Sri Lankan mangroves. However, this study focused only on the large bodied organisms while no attention was given to polychaetes or oligochaetes (Table 4.1). de Silva (1986) observed a scarcity of mangrove macrofauna both in abundance and diversity in the west coast mangroves of Sri Lanka compared to the wide range of fauna described in other countries. The fauna in these western mangroves was dominated by grapsid crabs and cerithidian gastropods.

Table: 4.1. List of reported mangrove macrofauna in Sri Lanka

Study	**Polychaetes**								**Crustaceans**																	**Gastropods**																	**Bivalves**				
	Eunicidae; *Eunice* sp	Nereididae; Nereidid	Pilargidiidae; Pilargidiid	Sphaerodoridae; Errantia	Heterospionidae; Heterospionid sp	Sabellidae; Sabellid	Syllidae; Sedentaria		*Thalamita crenata*	*Portunus pelagicus*	*Scylla serrata*	*Macrophthalmus depressus*	*Uca lacteal*	*Uca dussumieri*	*Neosermatium malbaricum*	*Metapograpsus messor*	*Chiromantes indiarum*	*Chiromantes bidens*	*Chiromantes darwinensis*	*Cardisoma carnifax*	*Sesarma* sp	*Sesarma thukuhar*	*Sesarma guttatum*	*Episesarma versicolor*	*Scylla serrata*		*Telescopium telescopicum*	*Terebralia palustris*	Cerithiidae; *Cerithidea cingulata*	*Cassidula musterina*	*Nerita polita*	*Littorina scabra*	Assimineidae; Assiminеid	Haminoeidae; Haminoeid sp	Hydrobiidae; Hydrobiid sp	Nassariidae; Nassariid sp	Naticidae; Naticid sp	Neritidae; Neritid sp	Planorbidae; Planorbidae sp	Terebridae; Terebrid sp	Thiaridae; Thiarid sp		Veneridae; *Meretrix casta*	Mytilidae; Mytilid sp	*Geloina coaxans*	*Saccostrea*	*Crassostrea madrasensis*
a									●	●	●	●	●	●	●	●	●	●	●								●		●	●	●												●		●	●	●
b	●	●	●	●	●	●	●																						●				●	●	●	●	●	●	●	●	●		●	●			
c																				●	●	●	●	●				●	●			●													●		●

a- Pinto (1986); b- Coastal conservation department Sri Lanka (2007); c- Dahanayaka and Wijeyaratne (2006)

4.1.3 Rationale for the current study

Mangrove restoration (encouraging the recovery of degraded areas formerly supporting mangroves) and habitat creation (the creation of new mangrove sites) is usually undertaken in order to restore or enhance one or more of the ecological functions of mangroves. Restoration of full ecosystem functioning would imply achieving similar macrofaunal communities to those seen at reference sites. Hence macrofaunal community structure might be a target of restoration activities. However, since the macrofauna can also be used as indicators of general ecosystem health, monitoring macrofauna communities might also provide a way of indirectly monitoring other mangrove functions. For example, mangroves may be planted in order to enhance sediment accumulation through dissipation of wave energy (Woodroffe, 1992; Furukawa and Wolanski, 1996; Furukawa *et al.*, 1997) and can change the properties of the substratum through organic components derived from leaf litters (Perry and Berkeley, 2009). Bioclastic material added by skeletal epifauna and infauna, including crabs and molluscs can also improve the sediment characteristics (Plaziat, 1974; Beaman *et al.*, 1994; Harvey *et al.*, 2001; Debenay *et al.*, 2002). These changes can positively influence micro-habitats for the macrofauna and hence increase macrofauna recruitment. Therefore, macrofauna might be considered as useful indicator groups in mangroves, as they are in other soft-bottom marine habitats (Whomersley *et al.*, 2008).

Differences in tree density could influence the recruitment of macrofauna in several ways. The relatively high litter fall could increase the particulate carbon in sediments which is useful for some fauna as food. During extreme low tides, the high density of trees could also provide shelter against desiccation (Ross and Underwood, 1997) while the complex structures within high density mangroves may also protect the animals from predators (Robertson and Blaber, 1992; Primavera, 1997) during high water.

Due to these reasons, high abundance and diversity of macrofauna at high mangrove densities might be expected. Conversely, the dense root structures of high tree densities may discourage the recruitment of some burrowing macrofauna species (Primavera, 1995) as it is difficult to construct burrows. In addition, high levels of particulate or dissolved organic matter increases the Total Organic Carbon (TOC) in marine sediments. The high TOC coupled with poor oxygenation produces anaerobic chemical conditions or high levels of ammonia and sulphide in the sediments (Magni *et al.*, 2009). The species richness, diversity and biomass of marine benthic communities are affected by the stress caused by TOC and the consequent sequence of responses is described in well studied models of organic enrichment (Pearson and Rosenberg 1978). In turn, this increases the microbial activity and reduces the redox potential of the sediments (Fenchel and Reidl, 1970). Eventually this results in the production of toxins such as hydrogen sulphide and methane. The altered status to anaerobiosis will limit the sedimentary macroinfauna in anoxic/reducing muds to species that are physiologically tolerant or that can form burrows or have other mechanisms to obtain their oxygen from the overlying water.

Alternatively, the moderate organic enrichment provides food to increase the abundance whilst greater enrichment declines the diversity with a few dominant pollution-tolerant opportunistic species such as the polychaetes *Capitella capitata* and *Manayunkia aesturina*. In very polluted intertidal areas (e.g. by hydrocarbon / petrochemical effluents), the anoxic sediment is defaunated and may be covered by sulphur-reducing bacteria (e.g.: *Beggiatoa* spp) affecting the palatability of the prey and thus impairing the functioning of marine areas (e.g. McLusky, 1982; Majeed, 1987). Hypernutrification of intertidal sand and mudflats may indicate eutrophication with colonization of opportunistic macroalgae such as *Enteromorpha*. The underlying sediments of these algal mats will become anoxic with reduced diversity and abundance of fauna (Simpson, 1997).

Since mangrove macrofauna have to survive varying salinity, high temperatures, anoxia and the threat of desiccation (Houbrick, 1991; Raffaelli and Hawkins, 1996) mature mangrove forests generally have relatively low infaunal diversity compared with open shallow marine habitats (Dittmann, 2001). This is probably because of the hypoxia (or anoxia) (Bosire *et al.*, 2008) associated with the organically rich sediments. In this respect, changes from an open to a mangrove dominated benthic habitat might be similar to those seen in studies of organic enrichment in the marine environment (Gray *et al.* 2002, Magni *et al.*, 2009). Under the classic Pearson and Rosenberg model, increased organic loading results in a decrease in diversity and body size, and a replacement of specialist with generalist species (Pearson and Rosenberg, 1978). This model is well tested in temperate waters (Nilsson and Rosenberg, 2000, Magni *et al*., 2009) but there are fewer examples of tropical studies (where higher average annual benthic production per unit of carbon is expected). The current study provides an opportunity to assess whether the Pearson and Rosenberg model is likely to apply to cases of enrichment with mangrove carbon. The study design, involving different densities of mangroves and thus different annual inputs of mangrove carbon per unit area, presents the opportunity of a ‘space for time’ substitution in which higher densities might represent more enriched points in the time series.

Although assessments have been carried out to compare macrofauna communities between natural and planted mangroves (Bosire *et al.*, 2004) time series data showing macrofaunal community development and change following planting is missing, and there are no studies comparing the effects of different mangrove densities on macrofauna abundance and composition. Hence filling this gap was the prime objective of the current study. In addition, it allowed an application of the Pearson and Rosenberg (1978) model to a case of organic enrichment by mangrove carbon.

4.1.4 Aims and Objectives

The aims of the current study were therefore;

1) To find the macrofauna community structure at different mangrove densities over time and then to review the optimum mangrove density for macrofauna.

2) To assess whether the Pearson and Rosenberg model is likely to apply to cases of organic enrichment with mangrove carbon. Understanding the responses of macrofauna community to changing mangrove density will be useful in managing mangrove planting activities with macrofauna in mind.

Therefore, the objectives of the current study are to conduct a three year long experiment with different mangrove density treatments along with unplanted controls and natural mangroves. Comparing the treatment and time effects on abundance, diversity and species richness of different macrofauna categories is the prime objective of this part of the study.

4.1.5 Null and Alternative Hypothesis for the current study

The specific hypothesis to be tested is:

Null hypothesis: Macrofauna community structure is unaffected by mangrove density

Alternative hypothesis: Macrofauna community structure depends on mangrove density

4.2 Materials and methods

The same *Rhizophora mucronata* plots prepared in four different densities 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2} for the sedimentation study at Palakuda, situated in Puttalam lagoon, Sri Lanka were also used for this study (see Chapter 2). Three 7.2 × 7.2m plots were also selected from a nearby natural mangrove forest for faunal comparisons. This was a monospecific *Rhizophora mucronata* natural forest and the three plots were covered by aerial root masses of approximately 20 years old, 12m high trees. Demarcated natural plots had nearly similar inundation frequencies and magnitudes as in planted plots.

Three data sets were collected, one in every September from 2007 to 2009; approximately 455, 850 and 1215 days after planting. At each time, a total of 72 samples were taken as four sub samples from each plot. A 5×5×5 cubic cm core was taken and washed over a 0.5-mm mesh. Organisms were preserved in 70% alcohol solution until enumeration and identification to the lowest possible taxonomic level under a dissecting microscope.

The organisms were broadly categorized in to crustaceans, oligochaetes, polychaetes and gastropods and their mean number m^{-2} for each replicate plot was calculated averaging its four sub samples. The Shannon-Weiner index ($H' = -\sum_{i=1} p_i \ln p_i$) was used for calculating the diversity of different taxa in each replicate. The organisms from each replicate were weighed to the nearest 0.01g and were averaged to wet biomass m^{-2} for each plot.

4.2.1 Univariate Analysis

Data were examined for normality and 'homogeneity of variances and transformed where necessary. The total abundance, total biomass, diversity and the abundance of each macrofaunal category were compared between treatments and times using repeated measures ANOVA (with treatments as the between-factor variable and time as the within-factor variable). Post-hoc tests were carried out where significant differences were found. For the animal groups that had significant time effects separate ANOVA tests were carried out for finding any treatment effect at individual times.

4.2.2 Multivariate Analysis

A biotic data similarity matrix using the Bray-Curtis similarity measure on non standardized-square-root transformed data was performed. Relationships obtained in the similarity matrix were displayed using non-metric multi-dimensional scaling (MDS) and a CLUSTER visualisation. Analyses of similarities (ANOSIM) tests were carried out for the differences between the time and the density groups. The

PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick 2001) and SPSS statistical packages were used for the analyses.

4.3. Results

4.3.1 Taxonomic Groups identified

23 groups of organisms (including Crustaceans, Annelids and Gastropods) with no crab species were identified during the study (Table 4.2). Tanaidae, *Nereis* sp, Capitellidae, Sabellariidae, Tubificidae *Cerithidea cingulata*, *Cerithidea* sp, *Hydrobia* sp, *Retusa* sp, *Nerita polita*, were recorded from all the treatments while *Cassidula* sp was found only in natural sites. *Lysidice* sp and Phyllodocidae were also recorded only from the highest (6.96) tree density.

Table: 4.2. Distribution of identified animal types at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka

Organism		Planting density m^{-2}					
		6.96	**3.26**	**1.93**	**0.95**	**Control**	**Natural**
	Crustaceans: Tanaidae	●	●	●	●	●	●
Polychaetes	Nereidae: *Neanthes* sp	●	●	●	●	●	
	Nereidae: *Nereis* sp	●	●	●	●	●	●
	Capitellidae	●	●	●	●	●	●
	Tomopteridae	●	●		●		
	Sabellariidae	●	●	●	●	●	●
	Terebellidae	●	●		●	●	
	Eunicidae: *Marphysa* sp	●	●	●			
	Eunicidae: *Lysidice* sp	●					
	Phyllodocidae	●					
	Polychaetes (Unknown)	●	●	●	●	●	
Gastropods	Potamididae *Cerithidea cingulata*	●	●	●	●	●	●
	Potamididae: *Cerithidea* sp	●	●	●	●	●	●
	Hydrobiidae: *Hydrobia* sp	●	●	●	●	●	●
	Retusidae: *Retusa* sp	●	●	●	●	●	●
	Littorinidae: *Littorina* sp	●	●	●	●	●	
	Neritidae: *Nerita polita*	●	●	●	●	●	●
	Skeneopsidae	●	●	●	●	●	
	Thaiididae	●		●	●	●	●
	Trochiidae	●	●	●	●	●	
	Ellobioidea: *Cassidula* sp						●
Bivalves	Corbiculidae: *Geloina* sp			●	●		
	Veneridae: *Meretrix* sp		●	●			
Oligochaets	Tubificidae	●	●	●	●	●	●
	Enchytraeidae	●	●	●	●	●	
	Hirudiniae	●		●	●		

4.3.2 Univariate Analysis

4.3.2.1 Total Macrofauna Abundance over time

The total macrofauna abundances in different treatments (excluding natural forest) showed significant differences with time (Table 4.3) but not with treatments (although differences did approach significance; Table 4.3). There were no significant time × treatment interactions ($p>0.05$) whilst the abundance showed a clear reduction in all the treatments after 850 days (Figure 4.1). Total abundance in the natural mangroves was very low; lower even than the unplanted controls. The reduction of the macrofauna abundance after the 850 days was also observed in the natural forest.

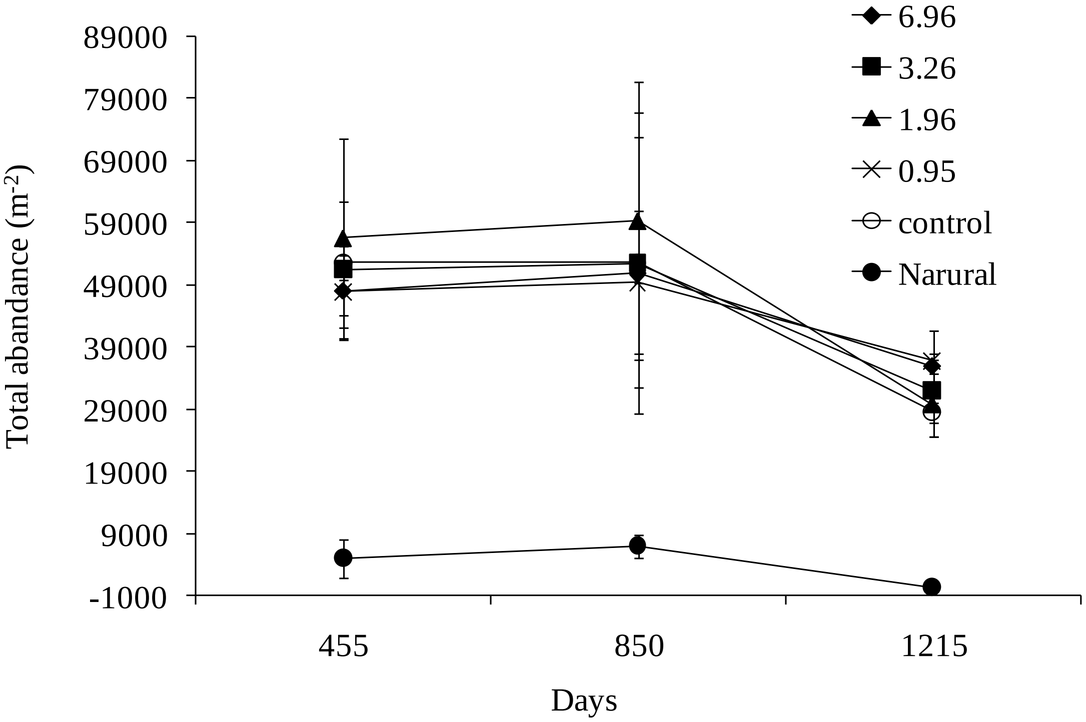


Figure: 4.1 Mean (± SE) total abundance of sediment macrofauna at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}.

Table: 4.3. Repeated measures ANOVA for total macrofauna abundance (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka

Source of variance	DF	MES	F value	P value
Time	2	2777120422	6.73	0.001
Treatment	4	1594111940	0.25	0.062
Time × Treatment	8	244085556	0.59	0.083
Error (Time)	20	411630257		
Error (Treatment)	10	63371126		
Total	44	5090319301		

Table: 4.4. Two-way ANOVA for total macrofauna abundance (at individual times) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Days	Source of variance	DF	SS	MES	F value	P value
455	Treatment	4	151353333	37838333	0.12	0.972
	Block	2	89233333	44616667	0.14	0.871
	Error	8	2536326667	317040833		
	Total	14	2776913333			
	S = 17806; R-Sq = 8.66%; R-Sq(adj) = 0.00%					
850	Treatment	4	228149345	570371667	0.41	0.800
	Block	2	960653456	48032667	0.03	0.967
	Error	8	111235665	1404455167		
	Total	14	1300038466			
	S = 37476; R-Sq = 17.47%; R-q(adj)=0.00%					
1215	Treatment	4	157492214	39373054	0.52	0.725
	Block	2	4560702	2280351	0.03	0.971
	Error	8	607890380	75986297		
	Total	14	769943295			
	S =8717; R-Sq =21.05%; R-Sq(adj) =0.00%					

4.3.2.2 Abundance of different Macrofauna taxa over time

The repeated measure ANOVA on the abundance of Gastropods showed a significant effect of time (Table 4.5) but not of treatments ($p>0.05$). The time × treatment interaction and the abundance at individual time also were not significant ($p>0.05$; Table 4.7). The oligochaetes abundance also differed significantly over time (Table 4.5) and showed a time × treatment interaction whilst the abundance did not differ between treatments ($p>0.05$). Oligochaete abundance at 455 and 850 days was not different between treatments whilst at the final time (1215 days) there was a significant difference ($p=0.05$; Table 4.6). The abundance in 0.95 treatment (13000 m^{-2}) was significantly higher (Table 4.6; Figure 4.2a) than the unplanted controls (4700 m^{-2}) at 1215 day. The polychaetes and crustaceans did not show significant effects of time or treatment ($p>0.05$).

Abundance of different animal types in different densities showed high interactions and varied largely with time. In natural plots on the other hand, the abundances were very low but were steady over time (Figure 4.2).

Table: 4.5. Repeated measures ANOVA for different macrofauna categories at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

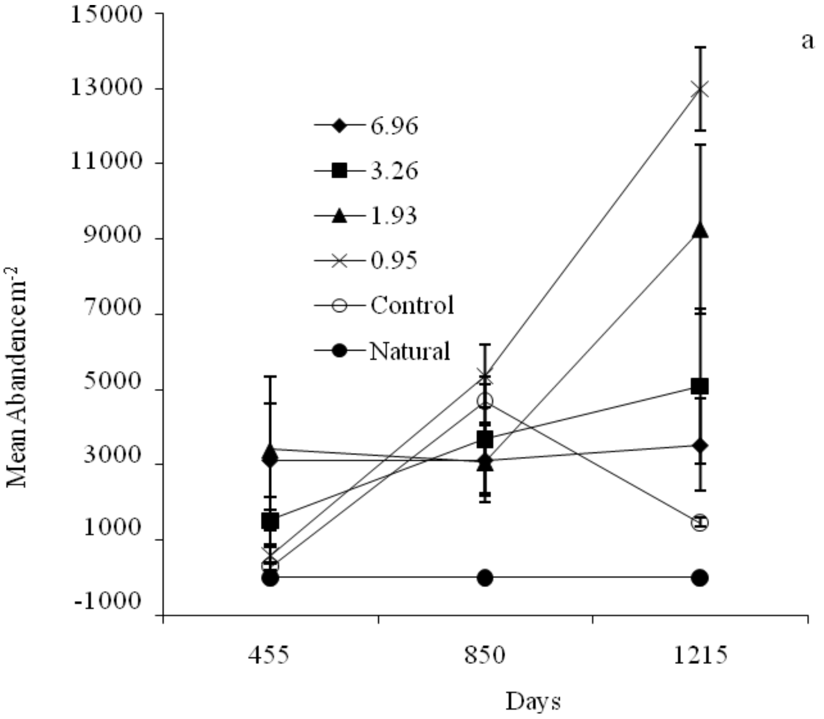
	Source of variance	DF	MES	F value	P value
Oligochaetes	Time	2	82232000	9.27	0.001
	Treatment	4	25092444.44	1.56	0.252
	Time × Treatment	8	24265611.11	2.14	0.031
	Error (Time)	20	8868555.55		
	Error (Treatment)	10	15998222.22		
	Total	44	156456833		
Gastropods	Time	2	5855410667	22.14	0.001
	Treatment	4	166804111.11	0.63	0.653
	Time × Treatment	8	38970111.11	0.15	0.991
	Error (Time)	20	264439222.21		
	Error (Treatment)	10	264834888.91		
	Total	44	6590459000		
Polychaetes	Time	2	1621555.55	3.50	0.493
	Treatment	4	492000	1.82	0.204
	Time × Treatment	8	551000	1.19	0.351
	Error (Time)	20	462111.11		
	Error (Treatment)	10	269111.11		
	Total	44	3395778		
Tanaids	Time	2	439514888.91	2.1	0.143
	Treatment	4	114171666.71	0.88	0.502
	Time × Treatment	8	138391000	0.67	0.711
	Error (Time)	20	204443444.41		
	Error (Treatment)	10	129454444.42		
	Total	44	1025975444		

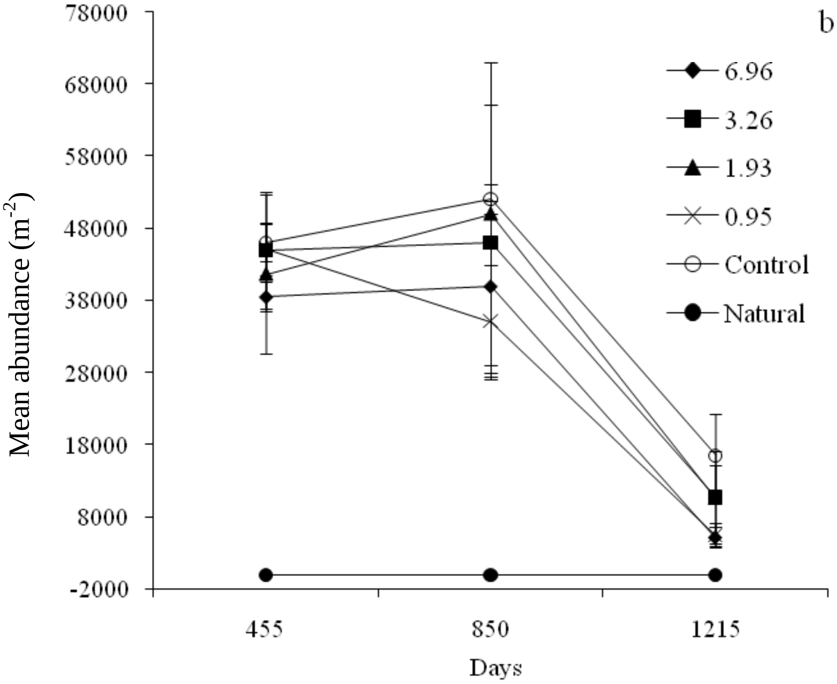
Table: 4.6. Two-way ANOVA for Oligochaete abundance (at individual time) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

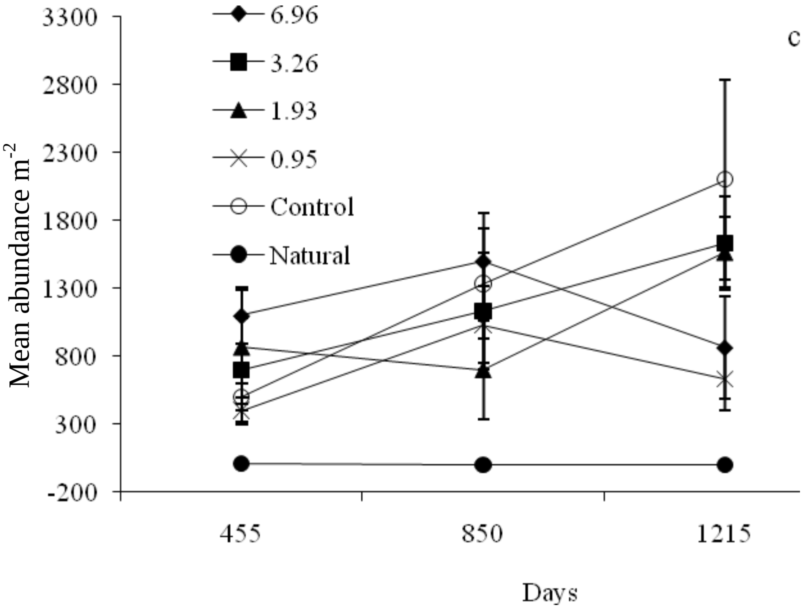
	Source of variance	DF	SS	MES	F value	P value
455	Treatment	4	24296000	6074000	0.57	0.693
	Block	2	9921333	4960667	0.46	0.645
	Error	8	85512000	10689000		
	Total	14	119729333			
	S = 3269; R-Sq = 28.58%; R-Sq(adj) = 0.00%					
850	Treatment	4	12209333	3052333	0.51	0.732
	Block	2	6465333	3232667	0.54	0.604
	Error	8	48114667	6014333		
	Total	14	66789333			
	S = 2452; R-Sq = 27.96%; R-q(adj)=0.00%					
1215	Treatment	4	257989333	64497333	3.63	0.050
	Block	2	45145333	22572667	1.27	0.332
	Error	8	142194667	17774333		
	Total	14	445329333			
	S =4216; R-Sq =68.07%; R-Sq(adj)=44.12%					

Table: 4.7. Two-way ANOVA for gastropod abundance (at individual day) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

	Source of variance	DF	SS	MES	F value	P value
455	Treatment	4	118550667	296337667	0.20	0.934
	Block	2	68585333	34292667	0.23	0.802
	Error	8	1211501333	151437667		
	Total	14	1398637333			
	S = 12306; R-Sq = 13.38%; R-Sq(adj) = 0.00%					
850	Treatment	4	596556000	149139000	0.20	0.931
	Block	2	152329333	76164667	0.10	0.902
	Error	8	5916444000	739555500		
	Total	14	6665329333			
	S = 27195; R-Sq = 11.24%; R-Sq(adj)=0.00%					
1215	Treatment	4	263870667	65967667	0.99	0.463
	Block	2	56064000	28032000	0.42	0.675
	Error	8	532209333	66526167		
	Total	14	852144000			
	S =8156; R-Sq =37.54%; R-Sq(adj) =0.00%					


a
Mean Abandence m^{-2}
15000
13000
11000
9000
7000
5000
3000
1000
-1000
455
850
1215
Days
6.96
3.26
1.93
0.95
Control
Natural


b
Mean abundance (m^{-2})
78000
68000
58000
48000
38000
28000
18000
8000
-2000
455
850
1215
Days
6.96
3.26
1.93
0.95
Control
Natural



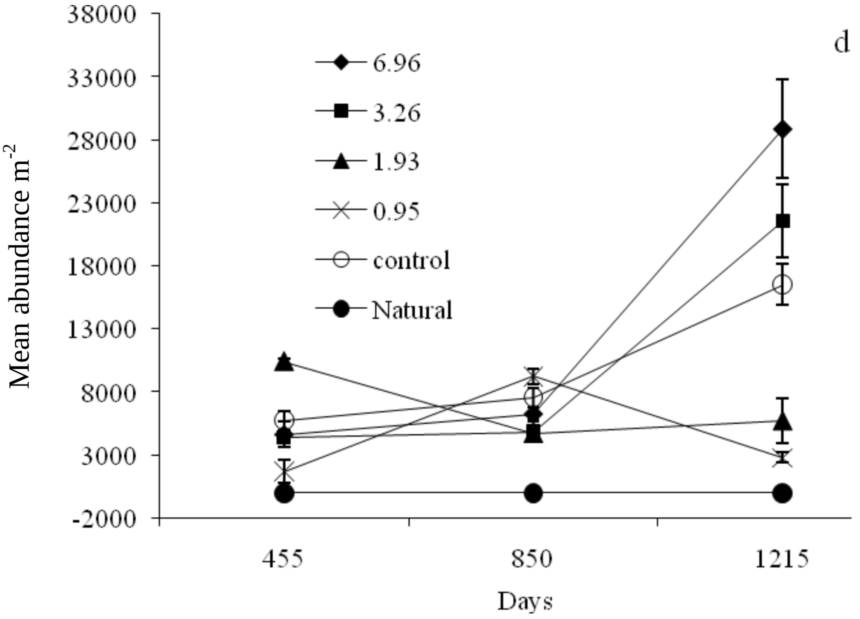


Figure: 4.2. Changes of different macrofauna taxa (Mean ± SE m^{-2}) over time at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2} (a) oligochaetes (b) gastropods (c) polychaetes (d) tanaidae

Since the changes of the total abundance of animals seemed to be driven largely by gastropods, another separate Repeated Measure ANOVA test was carried out excluding gastropods. The results showed a significant effect of time (Table 4.8) but not with treatments ($p>0.05$). The time × treatment interaction also was not significant ($p>0.05$).All the planted densities (excluding the controls) increased their macrofauna abundances (Figure 4.3) after 850 days. This implies that the observed decrease in total abundance (Figure 4.2) after 850 days could be attributed to reduction of gastropod community (Figure 4.2b).

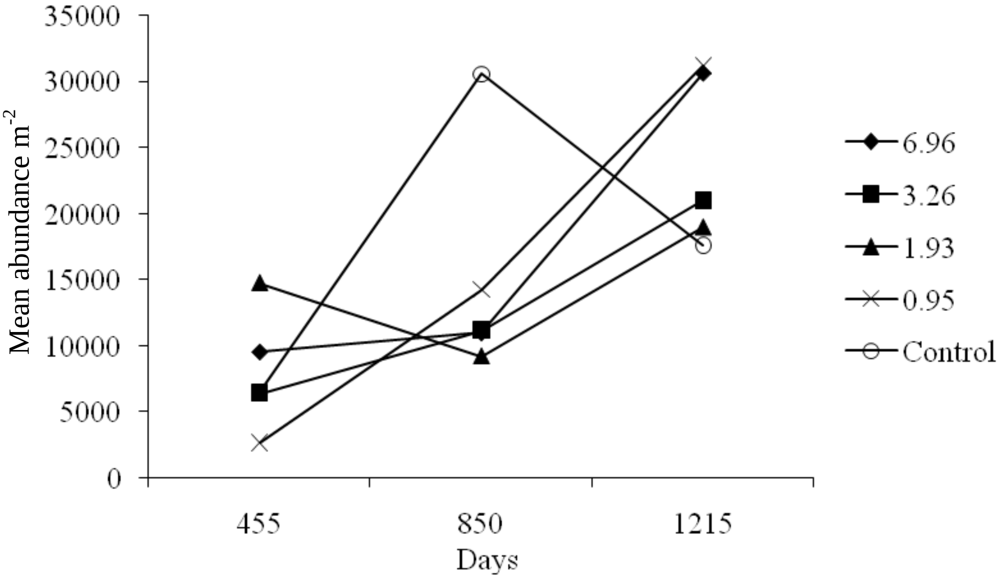


Figure 4.3 Mean (± S.E.) total abundance of sediment macrofauna (excluding gastropods) at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

Table: 4.8. Repeated measures ANOVA for total macrofauna (excluding Gastropods) abundance (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Time	2	948921555.61	7.47	0.041
Treatment	4	41255506.71	0.29	0.881
Time × Treatment	8	1888555590	1.48	0.222
Error (Time)	20	126957957		
Error (Treatment)	10	141383240.51		
Total	44	3147073850		

4.3.2.3 Total Biomass of Macrofauna

The total biomass of macrofauna showed significant reductions from 455 days to 1215 days in all the treatments, and there were significant time effects, but no treatment × time interaction (Figure 4.4; Table 4.9). The reduction of gastropod abundances (figure 4.2b) could also be attributed to reduction of total biomass as the relatively large shells could have largely contributed to the total biomass. Biomasses in natural plots were very low but steady over time.

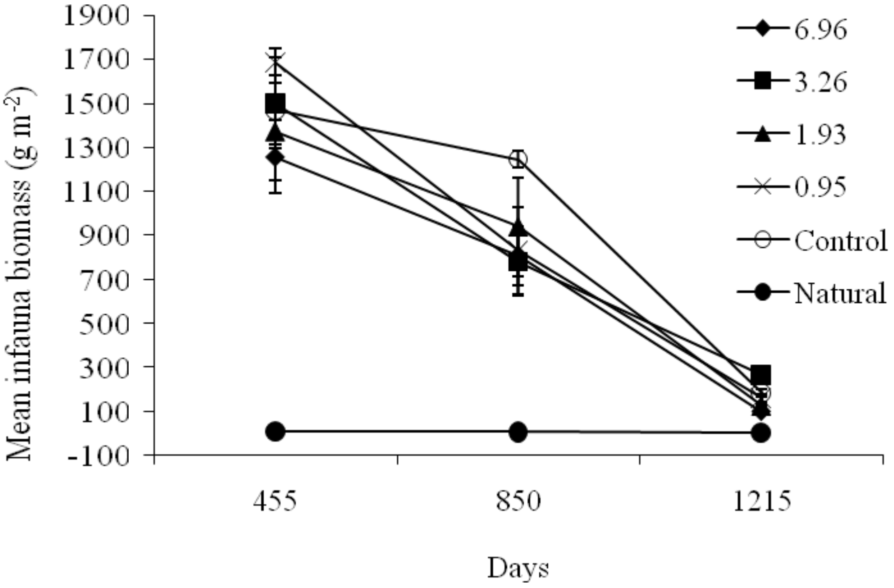


Figure: 4.4. Mean (± S.E.) total biomass of sediment infauna at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

Table: 4.9. Repeated measures ANOVA for total macrofauna biomass (gm^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Time	2	6353932.31	89.97	0.001
Treatment	4	62459.46	0.25	0.605
Time × Treatment	8	29480.28	0.88	0.544
Error (Time)	20	70619.77		
Error (Treatment)	10	63371126		
Total	44	5090319301		

4.3.2.4 Diversity of Taxa

The Shannon-Weiner Index ($H' = -\sum_{i=1} p_i \ln p_i$) showed significant changes over time and a significant time × treatment interaction (figure 4.5; table 4.10).

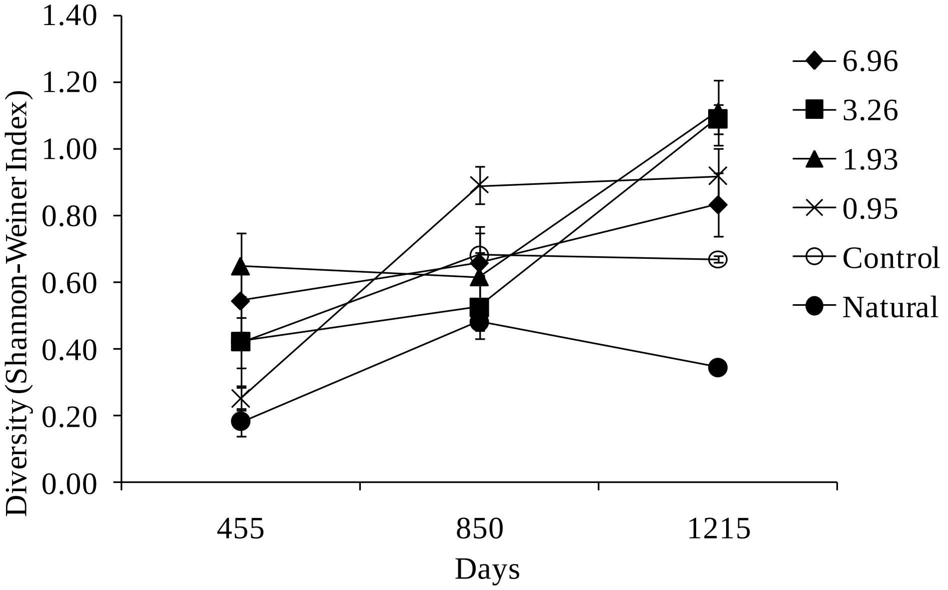


Figure: 4.5 Diversity (± S.E.) of sediment macrofauna at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

Table: 4.10. Repeated measures ANOVA for total macrofauna diversity at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Time	2	1.03	46.01	0.001
Treatment	4	0.21	0.90	0.493
Time × Treatment	8	0.71	3.15	0.001
Error (Time)	20	0.21		
Error (Treatment)	10	0.23		
Total	44	239		

4.3.3 Multivariate Analysis

The cluster analysis for the 455 days data (Figure 4.6) showed the degree of similarity of the macrofauna communities found in each replicate and demonstrated that the largest similarity (92.08%) occured between the 6.96 and 3.26, followed by 90% between 1.93-Control. Multidimensional scaling analysis (MDS) confirmed the high degree of similarity between 6.96-3.26 and between 1.93-Control, and this is shown by their clustered position in a specific region of multidimensional space**.**

The cluster analysis for the 850 days data (Figure 4.7) showed the degree of similarity of the macrofauna communities found in each replicate and demonstrated that the largest similarity (94.25%) occured between the 1.93 and control, followed by 93.01% between 0.95-Control. Multidimensional scaling analysis (MDS) confirmed the high degree of similarity between 1.93 and control and between 0.95-Control, and this is shown by their clustered position in a specific region of space (Figure 4.7).

The cluster analysis for the 1215 days data (Figure 4.8) showed the degree of similarity of the macrofauna communities found in each replicate and demonstrated that the largest similarity (95.21%) occured between the 1.93 and 0.95, followed by 85.55% between 3.26-Control. Multidimensional scaling analysis (MDS) confirmed the high degree of similarity between 1.93 and 0.95 and between 3.26-Control, and this is shown by their clustered position in a specific region of space (Figure 4.8).

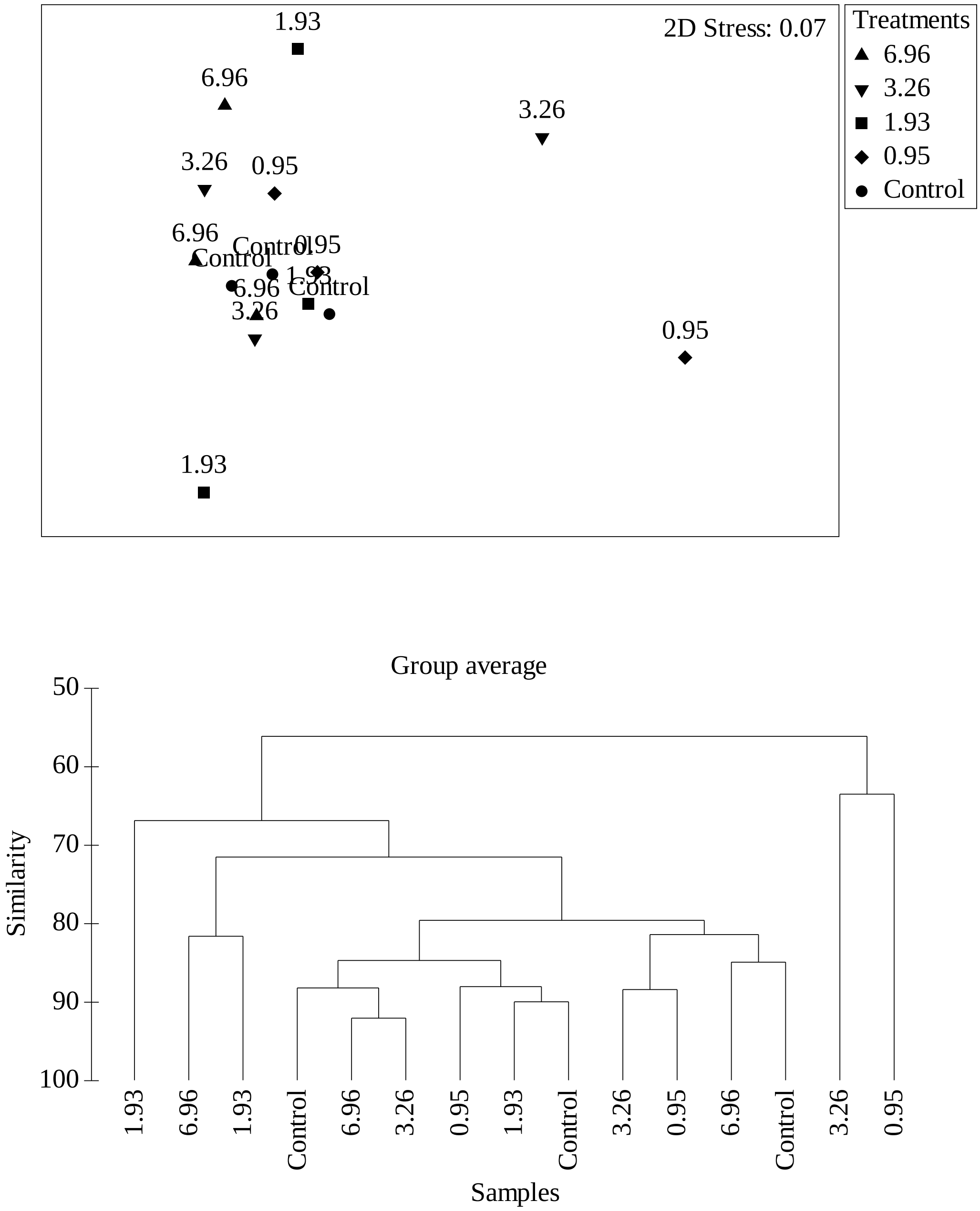


Figure: 4.6. MDS plot and the Cluster diagram for total macrofauna abundance (m^{-2}) of *R. mucronata* densities in Puttalam Lagoon, Sri Lanka; after 455 days of planting. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}

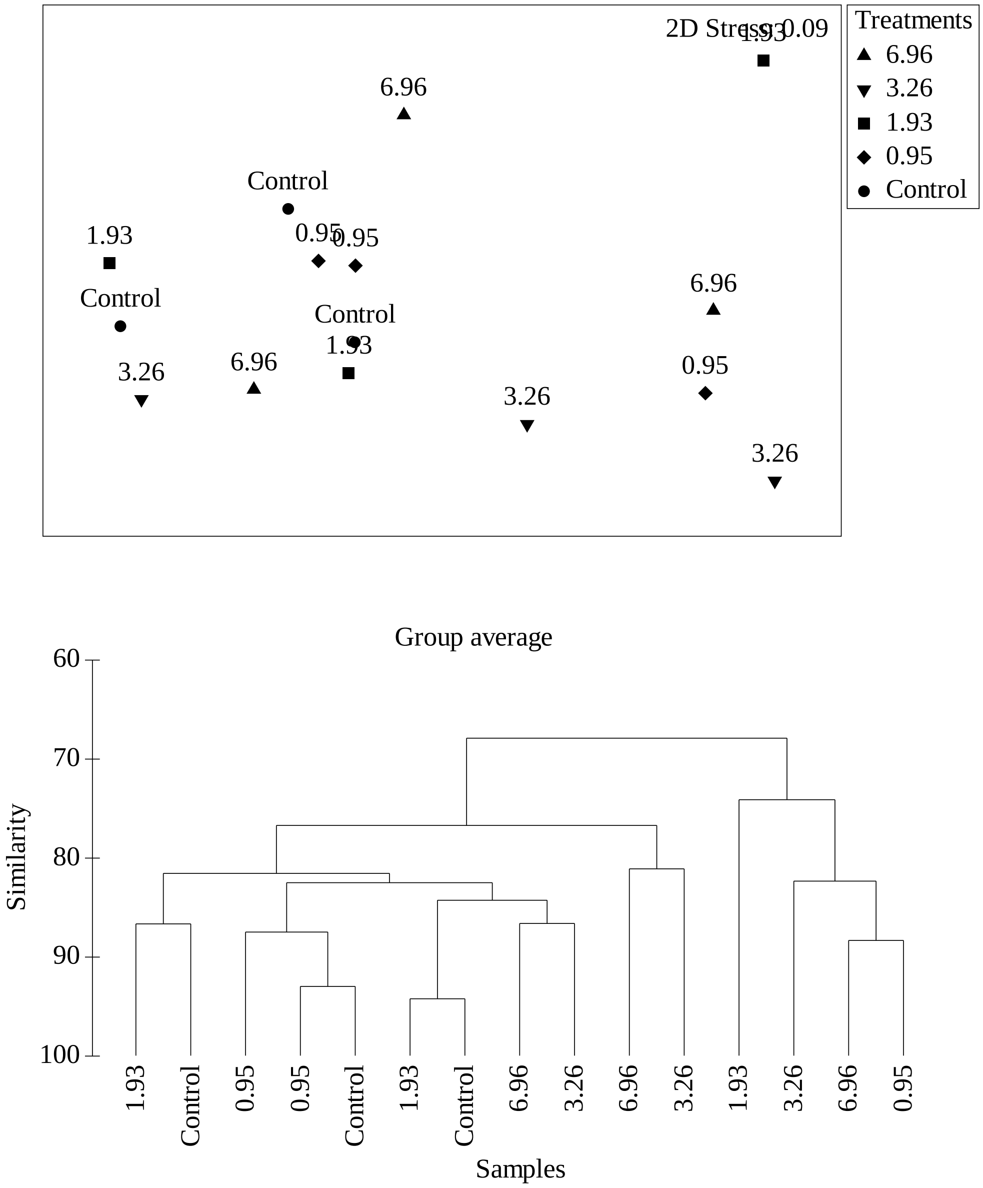


Figure: 4.7. MDS plot and the Cluster diagram for total macrofauna abundance (m^{-2}) of *R. mucronata* densities in Puttalam Lagoon, Sri Lanka; after 850 days of planting. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}.

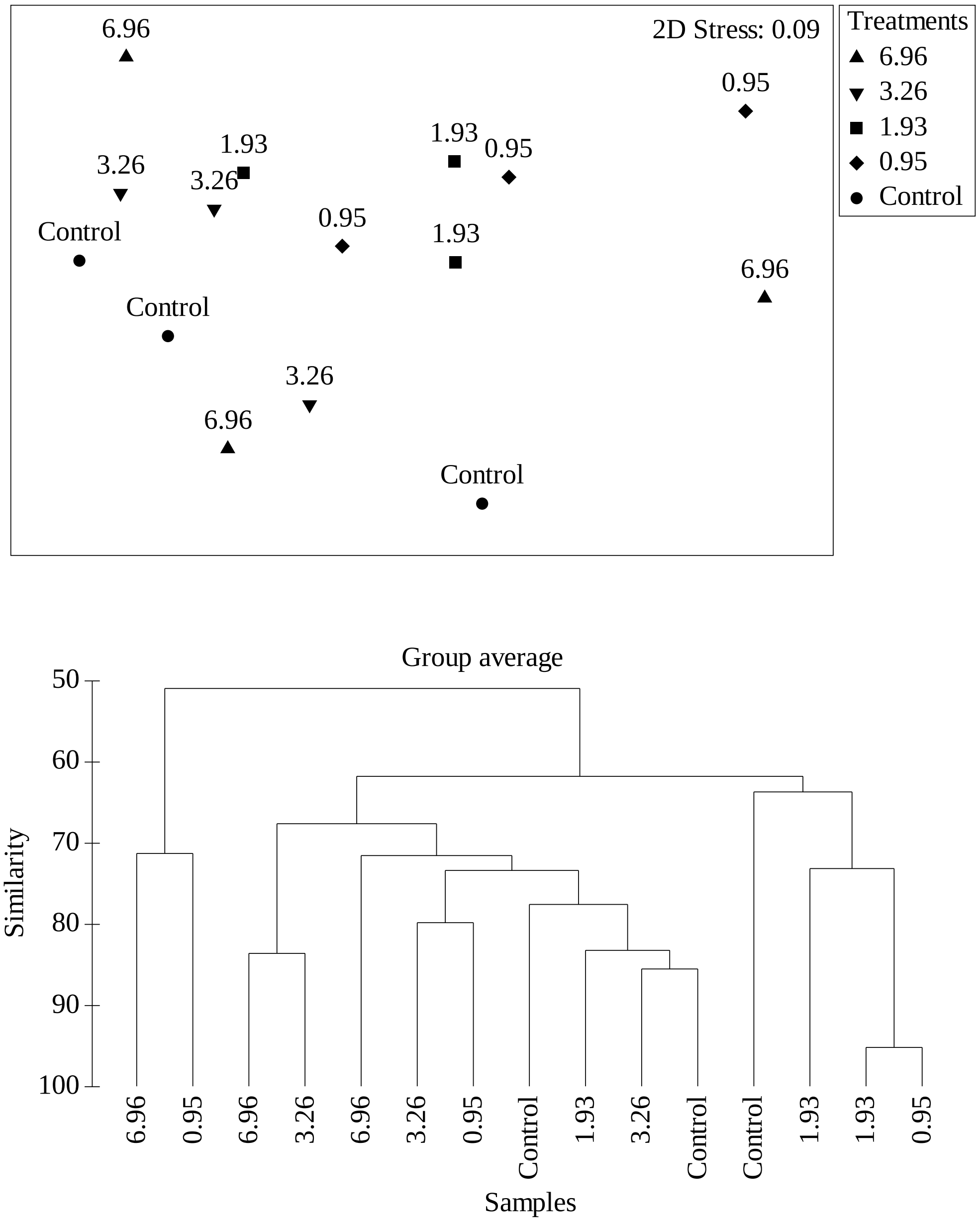
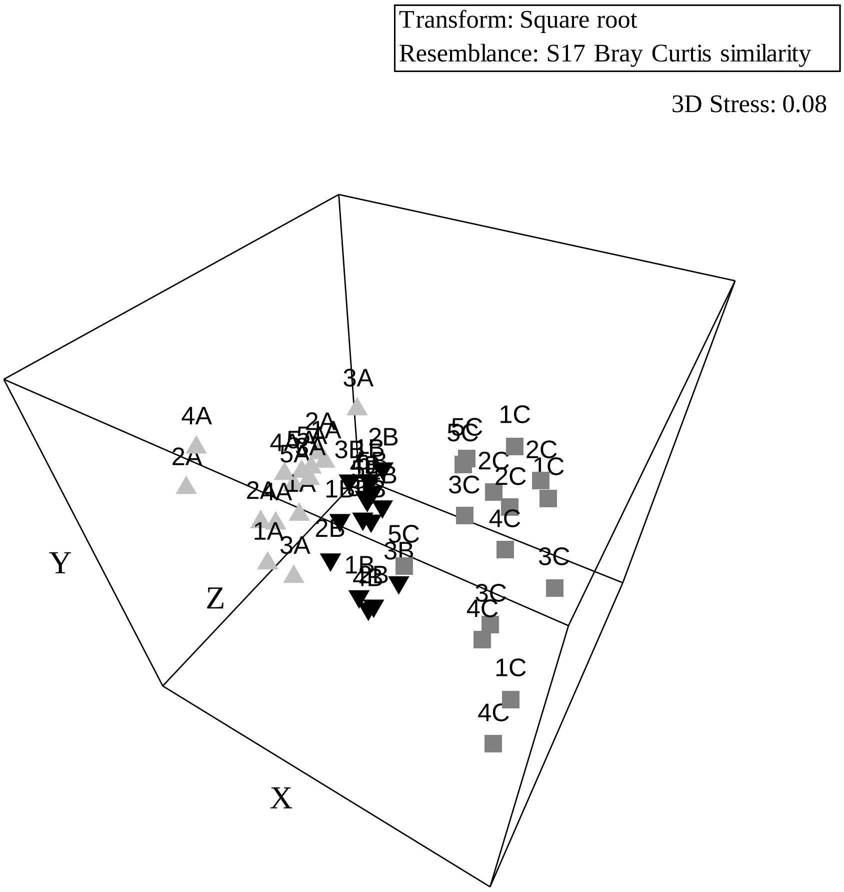


Figure: 4.8. MDS plot and the Cluster diagram for total macrofauna abundance (m^{-2}) of *R. mucronata* densities in Puttalam Lagoon, Sri Lanka; after 1215 days of planting. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}.

The MDS plot of different time with different densities (Figure 4.9) shows some clear separation of densities by 1215 days compared to the 455 and 850 days. This could be a sign that the different treatments have started behaving differently. However, some crowding of treatments was observed by 850 days. However, the results of the ANOSIM tests showed no differences between time or density groups (p>0.01).



X= Time (A= 455 days, B= 850 days, C= 1215 days)
Y= Treatments (1= 6.96, 2= 3.26, 3= 1.93, 4=0.95, 5= 0 seedlings m^{-2})
Z= Total macrofauna abundance (m^{-2})

Figure: 4.9. MDS plot for total macrofauna abundance (m^{-2}) changing over time; different *R. mucronata* densities, Puttalam Lagoon, Sri Lanka.

4.4 Discussion

No crabs were recorded during this study, which might reflect the relatively small sampling area (5X5-cm^{-2}) used, as they are highly active animals. In addition to the previously recorded *Cerithidea cingulata* (Pinto, 1986; Dahanayaka and Wijeyaratne, 2006; Coastal conservation department Sri Lanka, 2007) another *Cerithidea* sp was also identified during the study. This new *Cerithidea* sp resembled *Cerithidea cingulata* whilst it's shell was more globular at the body area, with a less conspicuous shell apex. Hence the entire shell was a little stout and the shell colour was also lighter compared to *Cerithidea cingulata* . *Nerita polita, Cassidula* sp. *Meretrix* sp, *Geloina* sp (Pinto, 1986), Hydrobiidae, Neritidae (Dahanayaka and Wijeyaratne, 2006, Dahanayaka, *et al*, 2007) and *Littorina* sp (Coastal conservation department Sri Lanka, 2007) were also observed. Polychaetes of *Nereis* sp, Capitallidae, Eunucidae, Sabellariidae from Sri Lankan marine environment (Dahanayaka and Wijeyaratne, 2006, Dahanayaka *et al*, 2007) were also found during the study. Unidentified species of Tanaidacea were also observed; members of this animal group have previously been recorded from Sri Lanka (Bamber *et al.*, 1996).

Although high abundance and diversity of macrofauna over the bare soil (resulted from cutting mangroves) have been recorded for 5year old planted mangroves (Bosire *et al.*, 2004) in Kenya, that has not been the case with planted mangroves in Palakuda, Puttalam Lagoon, Sri Lanka. The total infauna abundance in above 5year old *R. mucronata* plantation varied between 14×10^3 to 20×10^3 m^{-2} while in Palakuda planted treatments, it ranged between ~ 6×10^3 to 30×10^3 m^{-2} during the 1215 day study period. The 1.95 m^{-2} density showed both of these 5923 m^{-2} and 29679 m^{-2} abundances at 850 and 1215 days respectively (Figure: 4.1). Bosire *et al.*, (2004) studied the spatial variation of macrofauna abundance within replanted *R. mucronata* whilst this study has not addressed the changes of macrofauna abundance over time. Studying the changes of macrofauna over time in relation to the mangrove growth is important in terms of understanding the long term functionality of planted mangroves and the current study has covered the changes of macrofauna over the first 1215 days of mangrove growth. The surface area of the sediment samples for macrofauna analysis for Bosire *et al*., (2004) was 32.2 cm^{-2} which is 7.2 cm^{-2} larger than that of the current study (25 cm^{-2}) while the sampling depth for both studies was 5 cm. Irrespective of the small sampling area, the lowest macrofauna abundance of the current study (29679 m^{-2} in the 1.95 m^{-2} density at 850 days) exceeded the highest macrofauna abundance (20×10^3 m^{-2}) of planted *R. mucronata* in Kenya. The planting density for this Kenyan plantation is missing and it affects further comparisons with our density treatments.

The total macrofauna abundance or diversity of the 6.96 and 3.26 densities were not different from unplanted controls implying that even the high mangrove density plantations have not recruited more macrofauna over the bare soil. Absence of positive impacts from mangrove planting on macrofaunal abundance and diversity could be due to immaturity of young plants which may have not provided enough leaf litter for appropriate soil changes yet. The MDS plot of different time with different densities showed separation of densities by 1215 days compared to the 455 and 850 days (Figure 4.9) implying planted densities have started experiencing such a trend with increasing maturity.

However, the significant time effects on abundance of total macrofauna, Gastropods and Oligochaetes imply some environmental effects outside the experimental treatments. The significant time × treatment interaction of Oligochaetes indicates that the changes over time for each treatment differ between different treatments. At the final time (1215 days) there was a significant difference ($p=0.05$; Table 4.6) where the Oligochaete abundance in the 0.95m^{-2} treatment (13000 m^{-2}) was significantly higher than the unplanted controls (4700 m^{-2}) at 1215 day. The causes for these effects and interactions could be discovered through extending this study along with increasing the number of replicates.

The gastropod families observed during the study did not show any accumulation in planted mangroves and inhabited the bare soil instead (Figure 4.2b). These gastropods seem to have dispersed in to the open bare soil for their free grazing on soft sediments (rather than inside the crowded planted plots) as some benthos change their feeding distribution in response to sediments (Levin, 1984)

Varying the plant density has not increased the total macrofauna biomass m^{-2} due to not recruiting the fauna from the bare soil and hence the mangrove planting densities have not changed the biomass of sediment macrofauna. This also indicates that any of the planted mangrove density has not given significant benefit to sediment infauna. The positive connection between the mangrove leaf litter production and the sediment macrofauna community may not be applicable for flow-through systems where mangrove litter is not the dominant component of the sediment carbon due to receiving other suspended carbon from the lagoon or marine environment (Bouillon *et al,*. 2002; 2003). Since the Palakuda region of the Puttalam Lagoon is also a flow-through system with free water exchange, the changing mangrove density may not have influenced the levels of mangrove-derived carbon content in different treatments and hence the distribution of macrofauna. The mangrove-derived carbon does not become the major source of carbon for the benthic fauna when other sources of carbon are present (Bouillon *et al.*, 2002).

The reason for the clear reduction of the total macrofauna abundance in all the treatments after 850 days (Figure 4.1) is likely to be due to the reduction of gastropod abundance. The reason for this is not clear but since it occurred in all treatments it must be due to a general environmental change rather than an experimental effect.

4.5 Conclusions

None of the planted *Rhizophora mucronata* density in Puttalam lagoon have encouraged or discouraged recruitment of macrofauna over unplanted controls as a measure of total abundance, biomass or diversity over the initial 1215 days. The species richness, diversity and biomass of marine benthic communities are affected by the stress caused by organic enrichment in sediments (Pearson and Rosenberg 1978) and testing this for mangrove macrofauna was among the objectives of the current study. Although the levels of sediment carbon increased with increasing planting density, the unchanged diversity and biomass of macrofauna between the density treatments implies another process was operating that could mitigate the effect of the organic enrichment. The unfavourable toxicants (e.g. CH_4, NH_3, H_2S) concentrated from organic enrichment can change the sediment macrofauna in moderately deep marine sediments as the toxicants are not diluted or removed by the influence of the surface energy waves. Conversely, the shallow water and frequent wave exchanges in the Palakuda site is likely to remove these unfavourable toxicants mitigating any such effects of high carbon content accreted in to the sediments.

According to our δ^{13} C study of this site (chapter 5), the treatments showed mix of seagrass C and mangrove C in their sediments The %C in the sediments in the Palakuda planted mangroves varied between 0.54 to 0.68 and this range is very low compared to Alongi *et al*. (2004) where they have reported 27% sediment carbon for 5year old planted mangroves in Malaysia. Presence of very low %sediment carbon in Palakuda planted plots is likely to be the reason for not recruiting macrofauna from the open mudflat.

The natural mangroves also had very low abundance, biomass and diversity of macrofauna over the unplanted controls. The surface sediment of these natural mangroves had high fine root accumulations and this is likely to affect macrofauna as these fine roots may disturb their feeding and burrowing activities. However, analysis of abundance, biomass and diversity of macrofauna over a long period in planted treatments would result in community changes as a result of possible soil changes due to high litter fall and high underground root growth.

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CHAPTER 5- SEDIMENT CARBON SOURCES AND TEXTURE AMONG DIFFERENT MANGROVE TREE DENSITIES

5.1 Introduction

This chapter focuses on the characteristics of the sediment found in the experimental treatments at Palakuda, Puttalam Lagoon Sri Lanka. In particular it considers the sediment texture, carbon content and stable isotopic signature found at the site and examines differences in these variables between the treatments. The role of different tree densities in trapping carbon in their sediments is therefore considered, as is the likely origin of the carbon in sediments that are accreted.

5.1.1 Identification of the sediment carbon sources in Mangroves

^{13}C and ^{15}N stable isotopes and C/N ratio of the sediments are useful in identifying the major sources of carbon in mangrove sediments.

5.1.1.1 ^{13}C and ^{15}N Isotopes in Mangrove sediments

Mangroves are located in the land-sea transition zone receiving groundwater runoff, river discharge, tides and waves along with terrestrial, local, lagoonal and marine carbon sources mixed with sand, silt, clay and other inorganic particles (Wolanski, 1994; Ayukai and Wolanski, 1997). This suspended carbon from various sources coagulates and settles in to mangrove sediments along with other particles at the high tide as the slow water movement facilitates sediment accretion (Kristensen *et al.*, 2008). The increased bed roughness in mangroves, compared with open habitats, exerts higher drag forces on the incoming waves and thus slows water movements within the mangroves causing higher accretion of suspended sediments than in other habitats (Quartel *et al.*, 2007; Furukawa and Wolanski, 1996). The carbon in mangrove sediment may be derived from local sources (most obviously and importantly the trees themselves) but can also come from other marine habitats, from the land or may be anthropogenic (Bouillon and Boschker, 2005, Boonphakdee *et al.*, 2008). The sediment bulk organic content may also vary with the rate of sedimentation (Ishiwatari *et al.*, 1994). Mangroves located in deltaic systems with high river discharges or on coasts with high sediment current supply carrying fine allochthonous sediment particles in suspension will often trap large quantities of sediment and carbon, making alluvial plains (Othman, 1991). Thus mangroves are important interfaces for the coastal carbon cycle in tropical environments (Bouillon *et al.*, 2003).

Different taxa of plants synthesize organic carbon with distinct $^{13}C/^{12}C$ values (Table 5.1) due to isotopic discrimination by their photosynthetic enzymes and the regulation of diffusion resistance by their stomata (Schweizer *et al.*, 1999; Smith and Epstein, 1971). This carbon breaks down to detritus and mixes in to soil, water or sediments with little or no isotopic changes. The movements of sediments may transport this carbon to different locations while its original isotopic ratios remain unchanged. Hence, stable isotope ratios provide a means of tracing the origins of carbon in marine sediments. The ratio of carbon thirteen to carbon twelve is usually expressed using the $\delta^{13}C$ notation, defined as follows (Fry, 2006):

$$\delta^{13}C = [(^{13}R_{SAMPLE}/^{13}R_{STANDARD})-1] \times 1000$$

where; δ^{13} C = difference measurement made relative to standards (Stable carbon isotope signatures); R = the ratio of the heavy isotope to the light isotope for the element (^{13}C /^{12}C)

Carbon derived from mangrove litter and exudates typically has δ^{13}C values of around -29.75 to -27.64; hence when sediment is collected with values close to these it is likely to be dominated by mangrove carbon inputs (Prasad and Ramanadan, 2009), whilst less depleted signatures such as δ^{13} C = -22.4 are taken to imply higher marine influence (Bouillon *et al.*, 2007)

Where there are multiple sources of organic pools, as is often the case in mangrove sediments, the overlapping of isotopic signatures of different components can make ascertaining the source of the carbon difficult (Otero *et al.*, 2000; Cloern *et al.*. 2002; Prasad and Ramanadan. 2009); in such cases simultaneous measuring of more than one element (especially δ^{13} C and δ^{15} N) can overcome this difficulty (Bauer *et al.*, 2002).

The same equation described above can be used for reviewing the N from a specific source in mixed sediment where;

δ^{15} N= $[(^{15}R_{SAMPLE}/^{15}R_{STANDARD})-1] \times 1000$

δ^{15} N= difference measurement made relative to standards (Stable carbon isotope signature)

R= the ratio of the heavy isotope to the light isotope for the element (^{15}N /^{14}N)

Studies on the exchange of materials between the intertidal area and the water column help reveal the functioning of these systems (Flindt *et al.*, 2004) while understanding the sediment supply by different sources and the sites of deposition improves knowledge of coastal morphology (Balsinha *et al.*, 2009). However, most isotopic investigations tracing carbon sources in coastal sediments have been in temperate regions; relatively little is known of tropical systems (Barros *et al.*, 2010), particularly in mangroves (Bouillon *et al.*, 2003), and to my knowledge this is the third such study in Sri Lankan mangroves after Bouillon *et al.*, 2003 and 2004.

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5.1.2 C/N ratio in Mangrove sediments

The weight ratio of total organic carbon to total nitrogen (C/N ratio) is useful in determining the proportional contribution of different source of organic matter and as an organic source indicator in marine sediments (Kaushal and Binford, 1998; Prahl *et al.*, 1994; Sampei and Matsumoto, 2001). Different sources carry signatures with specific C/N ratios, for example: algae (between 4 and 10), terrestrial organic matter (greater than 20) (Meyers, 1994). The C/N ratio in marine organic matter often ranges from 6 to 9 due to the high protein content of contributing marine algae, phytoplankton and zooplankton (Müller, 1977; Prahl *et al.*, 1980; Krishnamurthy *et al.*, 1986; Uzaki and Ishiwatari, 1986). Hence, the C/N ratio in coastal sediments declines with higher proportions of phytoplankton products (Oviatt and Nixon, 1975; Cifuentes, 1991).

Conversely, the organic matter derived from higher vascular plants has very high C/N ratios (e.g. 78~179) because of high contents of non-protein lignin and cellulose that contain few nitrogen compounds (Eshiwatari *et al.*, 1977; Hedges *et al.*, 1986; Sampei and Matsumoto, 2001). For this reason, terrestrial organic inputs (C/N ~21) increase the C/N value in coastal sediments. The C/N ratio is therefore an effective and simple indicator of organic source, particularly in depositional coastal environments (Sampei and Matsumoto, 2001). However, biological alterations or digenetic processes in sediments may weaken the capacity of the C/N ratio to distinguish the original source of carbon (Thornton and McManus, 1994) as a drawback of this application. To overcome this constraint, C/N ratios combined with bulk organic δ^{13} C can provide an effective indicator for identifying coastal sediment sources (Yu *et al*., 2010). For instance, low C/N ratio coincident with less negative δ^{13} C signatures indicates sediments receiving marine or estuarine particulate suspended matter (Bouillon *et al.*, 2003).

Table: 5.1. Reported δ^{13}C, δ^{15}N and C/N values from various terrestrial and marine sources.

Source	**δ^{13}C ‰**	**δ^{15}N‰**	**C/N**	**Reference**
Algae	–18.7			Rodelli *et al.*, 1984
			4 to10	Meyers, 1984
Terrestrial organic matter			>20	
C_3 plants	-22 to –32			Smith and Epstein, 1971
C_4 plants	-8 to –18			
Whole plant of various mangroves		–2.6 to 1.89		Muzuka and Shunula, 2006
Rhizophora apiculata	–28.31	5.48	42.26	Prasad and Ramanadan, 2009
Mangrove leaf litter	–29.7 to –27.64			
Mangrove leaves (Fresh)	–26.9±1.0		33.1±6.9	Jennerjahn and Ittekkot, 1997
Mangrove leaves (senescent)	–27.1±1.3		78.5±16.3	
Mangrove sediments	–26.9±1.0		18.0±3.4	
	–22.4			Bouillon *et al.*, 2007
Riverine sediments	–23.8±1.1		17.6±10.8	Jennerjahn and Ittekkot, 1997
Continental Shelf sediments	–21.3±1.4		8.7±3.9	
Continental Slope sediments	–20.5±0.5		7.4±2.5	
Shelf suspended matter	–22.1±0.6		6.7±0.7	
Marine phytoplankton	–20 to –22			Fontugne and Duplessy, 1981
	–18 to –24			Fry and Sherr, 1984
Phytoplankton and zooplankton products			5 to 6	Bordowskiy, 1965a, b
	–21.0			Rodelli *et al.*, 1984
Seagrasses	–18.6 to –10.7			Bouillon *et al.*, 2004; Macia, 1995
	–3 to –19			McMillan, 1980
		0 to 8		Anderson and Fourqurean, 2003; Lepoint *et al.*, 2003; Marguillier *et al.*, 1998; Melville and Connolly, 2003; Vizzini and Mazzola, 2003.
		~10		Hemminga and Mateo, 1996
Organic matter of Marine origin (Algae, Phytoplankton, Zooplankton)			6 to 9	Müller, 1977; Prahl *et al.*, 1980; Krishnamurthy *et al.*, 1986; Uzaki and Ishiwatari, 1986
Riverrine / terrestrial			8-21	Mishima *et al.*, 1999
Freshly deposited planktonic organisms			6 to 9	Bordowskiy, 1965a; Prahl *et al.*, 1980; Biggs *et al.*, 1983

5.1.3 Sediment Textural composition in Mangroves

Sediments are mixtures of various sub-components (sand, silt, clay) of different particle sizes, shapes and weights. Hence different sub components have different flocculation / settling rates. Sediment texture refers to the proportions of sand, silt and clay below 2000 micrometers (2mm) in diameter in a bulk of sediment (Ivara, 1999; George *et al*., 2010). Sand is coarse and gritty, silt is smooth like flour and clay is sticky and plastic when wet (Davies and Abowei, 2009). The granulometry of sediments found in tidal wetlands like mangroves depends on physico-chemical parameters (Bhattacharya and Sarkar, 1996; Ramanathan *et al*., 2009) and is influenced by marine chemical cycles (Ronnie and Middelboe, 2004; Jahnke, 2005).

Ramanathan *et al*., (2009) reported the distribution of different sediment types according to the energy conditions in Sundarban mangroves, India. Different energy conditions lead to deposits of different kinds of sediments at different locations: muddy sand at high energy riverine zones, fine sands at moderately low energy levels and silt in rivers and creeks. Coastal bottom sediment reflects different hydrodynamic conditions, for example deposition of coarse particles at high energy shallow water locations and fine particles at low energy deeper places (Balsinha *et al*., 2009). According to Yang *et al*., (2008), tidal wetlands are capable of retaining fine grained sediments while unvegetated exposed tidal flats experience seasonal and storm-cyclic changes in sediment grain size. This is caused by: (a) plant obstructions attenuating the hydrodynamics facilitating the deposition of suspended sediments, (b) adherence of suspended sediments to plants, (c) prevention of wind-mediated re-suspension of fine grained deposits due to the protection from the vegetation canopy. The spatial and temporal variability of the sediment grain size is related to the biophysical (canopy and vegetation densities) interactions of hydrodynamics in the tidal wetland and the physical control of the un-vegetated flat.

The textural composition and the grain size distributions of tidal wetland sediments influences the nutrient, organic matter and water contents of sediments (Zhang *et al.*, 2002; Volkman *et al.*, 2000; Pasternack and Brush, 2001; Uncles *et al.*, 1998). It also determines the local biogeochemistry (Ronnie and Middelboe, 2004; Dylan and Dahlgren, 2005; Zhou *et al.*, 2007) and distributions of soft bottom animals like polychaetes and shrimps (Sanders, 1958; Woodin, 1978; Nel *et al.*, 1999; Ysebaert *et al.*, 2003; Ikomi *et al.*, 2005; Atobatele *et al.*, 2005). The energy required for constructing burrows and the stability of the constructed burrow heavily depends on the sediment structure. Intraspecific variation of burrows has been observed depending on the types of the substrate (Karplus, 1987). Therefore, studying the sediment texture under different tree densities would help provide basic understanding of how different tree densities would produce different sediment textures preferred by different types of fauna. The field of mangrove restoration still lacks this knowledge and the current study can help address this issue as a part of the sediment textural study.

Since natural mangroves have various configurations of densities, different regions of the forest would experience different hydrological energies and hence would facilitate the deposition of different suspended components at different places in the forest as described by Yang *et al.* (2008). The surface sediment accretion process is important for mangroves elevating the soil against rising sea-level (Kumara *et al.*, 2010) and sediments with weak texture (dominated by sand) would be eroded easily with high wave actions (Yang *et al.*, 2008). Conversely, sediments dominated by clay would give more resistance to coastal erosion while they would also facilitate binding more nutrients to sediments. Therefore, understanding the texture of sediments under different mangrove densities will help in manipulating mangrove plantations for better accretion of more resistant sediments to erosion and depletion of soil nutrients. Conducting such a controlled experiment is yet to be done and filling this research gap is among the current research objectives.

5.1.4 Aims and Objectives of the study

The aims of the current study are therefore to study the carbon content, carbon sources and texture of sediments under different mangrove densities. The results of the study are aimed to review the significance of mangrove planting density on capturing the coastal carbon and changing the sediment characteristics in favour of macrofauna or reducing coastal erosion.

The objectives of the current study are studying the %C, C/N ratio, $\delta^{13}C$, $\delta^{15}N$ (‰) and texture of the sediment under high, medium and low planting densities (with sufficient numbers of replicates) along with unplanted controls.

5.1.4 Null and Alternative Hypothesis for the current study

The following hypothesis will be tested under this part of the study.

Null hypothesis: %C, C/N ratio, $\delta^{13}C$, $\delta^{15}N$ (‰) and sediment texture are independent from mangrove tree density

Alternative hypothesis: Above parameters depend on mangrove density

5.2 Materials and methods

5.2.1. C, N, C/N ratio, δ^{13}C and δ^{15}N in different Mangrove densities

The same *Rhizophora mucronata* plots prepared in four different densities (6.96, 3.26, 1.93, 0.95, and 0 (control) seedlings m^{-2}) for the sedimentation study at Palakuda, situated in Puttalam lagoon, Sri Lanka were also used for this study. After 880 days (or approx. 2.4 years) from plantation establishment, four sediment surface scrapes (1-cm depth × 10 x10-cm area) were taken from random points within each quarter of every plot and combined to give one sample per replicate. Samples were were then dried and were exported to the Environmental engineering Research Center, Queen`s University of Belfast (UK) for further analysis. At the laboratory, the sediment samples were completely dried in an electric oven at 60°C and they were ground to fine powder using a Wiley mill. All the samples were subsampled for carbon, (%) and δ^{13}C, δ^{15}N (‰) analysis.

The subsamples for δ^{13}C analysis were washed with dilute HCl to remove possible carbohydrates and were re-dried. Subsamples for δ^{15}N were not subjected to this treatment as the acidification affects the δ^{15}N values (Bunn *et al.*, 1995; Pinnegar and Polunin, 1999). Samples for δ^{13}C and δ^{15}N analysis were similarly combusted in the Elemental analyzer, coupled to isotope mass spectrometer via an open split interface. The relative abundance of the heavy and light isotopes of C and N were expressed as δ^{13}C and δ^{15}N (‰) values by integrated computer.

Samples were preheated at 105°C to record the dry weight and then they were combusted in a muffle furnace at 900°C to a constant weight. The %C in samples were determined as the dry weight loss during the combustion and the previously calculated % sediment N values (in chapter 3) were combined with the % C values to calculate the C/N ratios.

5.2.2. Texture of the sediments

The % values of clay, very fine silt, fine silt, medium silt, coarse silt, very fine sand, fine sand, medium sand, coarse sand and very coarse sand were estimated through Laser Diffraction Particle Size Analysis (LDPSA). In the Laser Diffraction Particle Size Analysis method, the dried sediment sample is passed through an expanded laser beam and the light scattered by different particles is collected over a range of angles by a photosensitive detector. The angles of diffraction are inversely related to the particle size and then the distribution of scattered intensity is analyzed by a computer to yield the particle size distribution. Laser Diffraction Particle Size Analysis for the sediment samples of the current study were conducted at the Environmental engineering Research Center, Queen`s University of Belfast (UK).

5.2.3. Statistical Analysis

Data were examined for normality and homoscedasticity of residual variances, and transformed where necessary. The C (%), N (%), C/N and $\delta^{13}C$, $\delta^{15}N$ (‰) were compared between treatments using Two-way ANOVA. Post-hoc tests were carried out where significant differences were found.

5.3 Results

5.3.1. %C in sediments

Two-way ANOVA with treatments and blocks as factors showed that % C in sediments differed significantly among different mangrove densities and between blocks (Table 5.2). For the highest density of 6.96 seedlings m^{-2} the % C (mean ± SE) was 0.68 (± 0.04) while the % C values for 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were 0.55 (± 0.08), 0.53 (± 0.05), 0.54 (± 0.04), and 0.46 (± 0.05), respectively (Figure 5.1). Tukey`s comparisons showed a significantly higher %C in the highest (6.96 seedlings m^{-2}) tree density compared to the unplanted controls. There were no significant differences in the sediment %C between the other treatments.

5.3.2. C/N ratio in sediments

Two-way ANOVA with treatments and blocks as factors showed that C/N sediments differed significantly among different mangrove densities but not between blocks (Table 5.3). C/N ratios for 6.96, 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were 9.01 (± 0.52), 8.53 (± 0.35), 7.85 (± 0.53), 7.88 (± 0.51), and 9.32 (± 0.72), respectively. According to the Tukey`s comparisons, unplanted controls were significantly different from 1.93 and 0.95 densities.

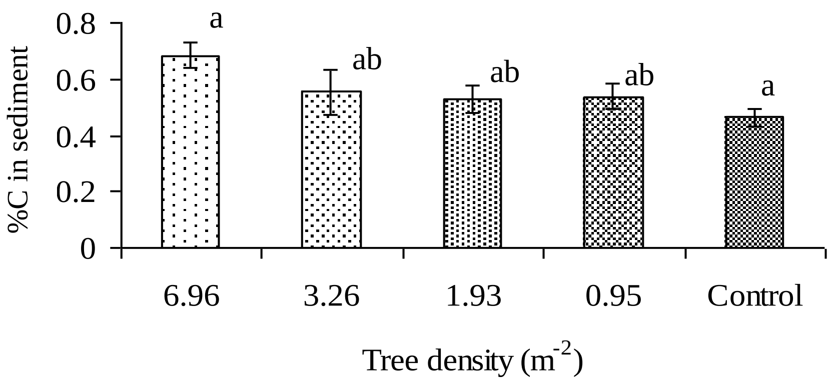

Figure: 5.1. %C (± S.E.) of sediment at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 880 days of planting. Bars represented by different letters identify significantly different %C in sediments at $\alpha = 0.05$.

Table 5.2 Two-way ANOVA for mean % sediment carbon at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka: after 880 days of planting.

Source of variance	DF	SS	MES	F value	p value
Treatment	4	0.08	0.02	5.09	0.025
Block	2	0.04	0.02	6.58	0.020
Error	8	0.03	0.00		
Total	14	0.16			

S = 0.06; R-Sq =80.73%; R-Sq(adj) = 66.28%

Table: 5.3. Two-way ANOVA for mean sediment C/N ratio at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka: after 880 days of planting.

Source of variance	DF	SS	MES	F value	p value
Treatment	4	5.20	1.30	3.79	0.052
Block	2	0.13	0.06	0.20	0.822
Error	8	2.75	0.34		
Total	14	8.09			

S = 0.58; R-Sq =66.02%; R-Sq(adj) = 40.54%

5.3.3. $\delta^{13}C$ signature in sediments

Two-way ANOVA test showed no significant differences in the ‰ $\delta^{13}C$ in sediments among different mangrove densities (Table 5.4). The ‰ $\delta^{13}C$ for 6.96, 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were -16.13 (± 0.95), -15.85 (± 0.97), -15.71 (± 0.40), -16.41 (± 0.14), and -14.58 (± 0.30), respectively.

Table: 5.4. Two-way ANOVA for mean sediment ‰ $\delta^{13}C$ values at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka: after 880 days of planting.

Source of variance	DF	SS	MES	F value	p value
Treatment	4	5.92	1.48	0.99	0.465
Block	2	0.76	0.38	0.25	0.783
Error	8	11.95	1.49		
Total	14	18.63			

S = 1.22; R-Sq =35.85%; R-Sq(adj) = 0.00%

5.3.4. $\delta^{15}N$ signatures in sediments

Two-way ANOVA with treatments and blocks as factors showed no significant differences among different mangrove densities in the ‰ $\delta^{15}N$ in sediments (Table 5.5). The ‰ $\delta^{15}N$ for 6.96, 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were 2.80 (± 0.13), 2.73 (± 0.29), 2.40 (± 0.24), 2.41 (± 0.22), and 2.49 (± 0.11), respectively.

Table: 5.5. Two-way ANOVA for mean sediment ‰ $\delta^{15}N$ values at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka: after 880 days of planting.

Source of variance	DF	SS	MES	F value	p value
Treatment	4	0.42	0.10	1.42	0.311
Block	2	0.66	0.33	4.51	0.049
Error	8	0.59	0.07		
Total	14	1.66			

S = 0.27; R-Sq =64.76%; R-Sq(adj) = 38.33%

The $\delta^{15}N$ *vs.* $\delta^{13}C$ plot drawn for the sediment from different density treatments of *Rhizophora mucronata* (Figure 5.2) showed that all the treatments (including unplanted controls) fall in the bottom left corner of the seagrass box. The $\delta^{13}C$ and $\delta^{15}N$ signatures of the sediments of the planted plots ranged from -15.71 to -16.41 and 2.40 to 2.80 respectively.

5.3.5. Sediment Texture

Although there was a tendency for a greater proportion of fine materials (silt) with increasing tree density, differences between treatments in the various categories of sediment size were significant only for medium sand (Table 5.7; Figure 5.3).

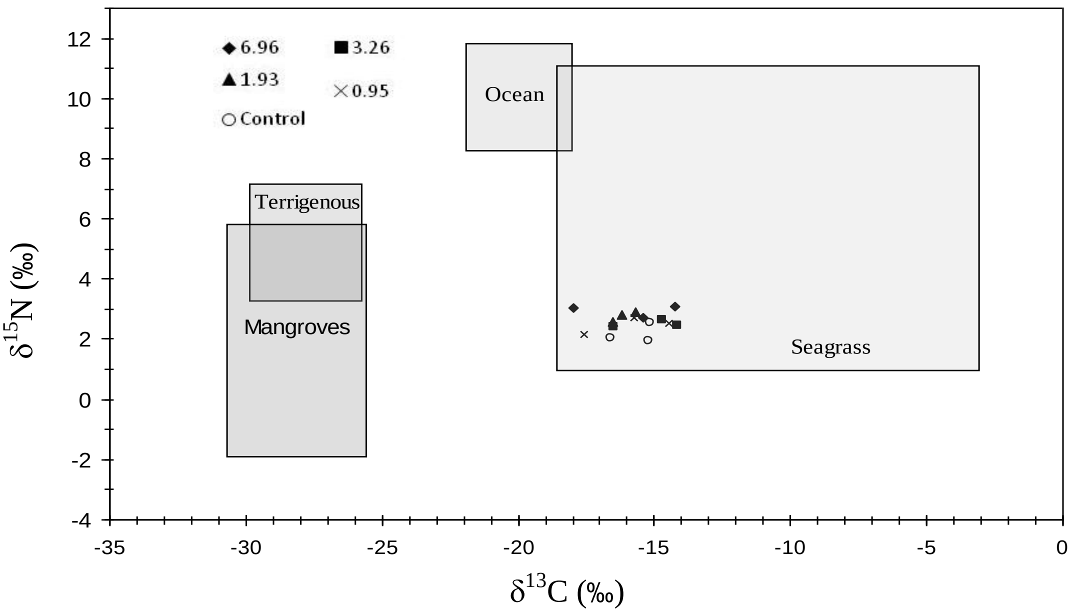

Figure: 5.2. Position of different *R. mucronata* density treatments (Puttalam Lagoon, Sri Lanka) within a $\delta^{15}N$ *vs.* $\delta^{13}C$ plot of potential sources. Different symbols indicate different treatments. **Sources used for producing the limits of the shaded boxes:** McMillan, 1980; Fontugne and Duplessy, 1981; Fry and Sherr 1984; Meyers, 1984; Macia, 1995; Hemminga and Mateo, 1996; Jennerjahn and Ittekkot, 1997; Marguillier *et al.*, 1998; Anderson and Fourqurean, 2003; Lepoint *et al.* 2003; Melville and Connolly, 2003; Vizzini and Mazzola, 2003; Bouillon *et al.*, 2004; Muzuka and Shunula 2006; Prasad and Ramanadan 2009; Barros *et al.* 2010.

Table 5.6: Different sediment components (% values ± SE) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka: after 880 days of planting and the p values obtained from Two-way ANOVA test.

Component	6.96	3.26	1.93	0.95	Unplanted control	P Value
Clay	0.32±0.05	0.28±0.13	0.18±0.06	0.19±0.06	0.14±0.04	0.451
Very Fine Silt	2.54±0.15	2.41±0.47	2.09±0.21	2.12±0.26	1.79±0.15	0.331
Fine Silt	2.54 ±0.08	2.46±0.37	2.24±0.16	2.26±0.21	1.95±0.13	0.304
Medium Silt	2.92±0.05	2.86±0.41	2.56±0.16	2.63±0.17	2.35±0.14	0.333
Coarse Silt	11.80±0.53	10.79±0.83	9.09±0.98	9.85±0.66	8.49±0.76	0.254
Very Fine Sand	7.13±0.35	5.60±0.41	4.93±0.16	5.16±0.59	4.21±0.58	0.091
Fine Sand	13.63± 1.49	15.67±1.50	13.16±0.50	15.63±1.06	15.72±1.4	0.321
Medium Sand	35.77±1.15	38.95±2.24	38.34±1.98	39.95±1.92	42.37±1.5	0.043
Coarse Sand	22.87±1.45	20.77±3.93	26.61±1.25	21.91±2.04	22.76±1.9	0.475
Very Coarse Sand	0.45±0.26	0.21±0.12	0.79±0.12	0.30±0.19	0.18±0.16	0.202

Table: 5.7. Two-way ANOVA for different sediment components at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka: after 880 days of planting

Table 5.7 continue..

	Source of variance	DF	SS	MES	F value	P value
Clay	Treatment	4	0.07	0.02	1.01	0.458
	Block	2	0.03	0.02	1.00	0.409
	Error	8	0.14	0.02		
	Total	14	0.24			
	S = 0.13; R-Sq = 42.96%; R-Sq(adj) = 0.19%					
Very Fine Silt	Treatment	4	1.02	0.26	1.33	0.339
	Block	2	0.71	0.35	1.84	0.220
	Error	8	1.54	0.19		
	Total	14	3.28			
	S = 0.44; R-Sq = 52.92%; R-Sq(adj)=17.61%					
Fine Silt	Treatment	4	0.61	0.15	1.46	0.301
	Block	2	0.54	0.27	2.56	0.138
	Error	8	0.84	0.10		
	Total	14	1.99			
	S =0.32; R-Sq =57.79%; R-Sq(adj) =26.13%					
Medium Silt	Treatment	4	0.62	0.15	1.35	0.331
	Block	2	0.56	0.28	2.45	0.148
	Error	8	0.92	0.11		
	Total	14	2.11			
	S = 0.34; R-Sq = 56.28%; R-Sq(adj) =23.48%					
Coarse Silt	Treatment	4	21.18	5.29	1.64	0.255
	Block	2	7.88	3.94	1.22	0.344
	Error	8	25.78	3.22		
	Total	14	54.85			
	S = 1.79; R-Sq = 52.99%; R-Sq(adj) = 17.74%					
Very Fine Sand	Treatment	4	14.20	3.55	2.92	0.092
	Block	2	15.16	7.581.2	6.22	0.023
	Error	8	9.74	1		
	Total	11	1756744			
	S= 1.23; R-sq= 53.88; R-sq (adj)= 26.12%					

	Source of variance	DF	SS	MES	F value	P value
Fine Sand	Treatment	4	18.97	4.74	1.36	0.328
	Block	2	19.92	9.96	2.86	0.116
	Error	8	27.85	3.48		
	Total	14	66.75			
	S = 1.86; R-Sq = 58.27%; R-Sq(adj) = 26.98%					
Medium Sand	Treatment	4	69.44	17.36	3.93	0.047
	Block	2	62.53	31.26	7.08	0.017
	Error	8	35.31	4.41		
	Total	14	167.28			
	S = 2.101; R-Sq = 78.89%; R-Sq(adj)=63.06%					
Coarse Sand	Treatment	4	57.83	14.45	0.96	0.478
	Block	2	41.07	20.54	1.37	0.309
	Error	8	120.28	15.03		
	Total	14	219.19			
	S =3.878; R-Sq =45.12%; R-Sq(adj) =3.97%					
Very Coarse Sand	Treatment	4	0.74	0.18	1.88	0.208
	Block	2	0.19	0.09	0.96	0.422
	Error	8	0.79	0.09		
	Total	14	1.72			
	S = 0.31; R-Sq = 54.11%; R-Sq(adj) =19.69%					

5.4 Discussion

The %N reported from Palakuda planted plots (0.066 to 0.076%; chapter 3) were comparatively low compared to Kenyan (0.01 to 3.55%) and Belize (0.9%) mangroves (Middelburg *et al*. 1996; Wooller *et al*., 2003). Complex coastal systems like mangroves receive carbon from terrestrial and oceanic sources creating mangrove sediments with different δ^{13}C signatures. On the other hand, the N components in mangrove sediments undergo various nitrogenous processes such as mineralization, nitrification, volatization, denitrification and isotope fractioning and produce a wide range of δ^{15}N signatures (typically 0 to ~13) (Högberg, 1997; Tucker, e*t al*., 1999; Voss *et al*., 2005; Hu *et al*., 2006). For constraining a wide range of carbon sources in coastal sediments, the classic δ^{15}N *vs.* δ^{13}C plot is used because the δ^{13}C axis ranges from terrestrial (more negative) to marine (higher) values (Cifuentes *et al*., 1996; Andrews *et al*., 1998; Fisher *et al*., 1998; Bouillon *et al*., 2000; Dehairs *et al*., 2000; Maksymowska *et al*., 2000; Graham *et al*., 2001; Carreira *et al*., 2002; Goñi *et al*., 2003; Barros *et al*., 2010) while the δ^{15}N axis also represents a sufficient range of δ^{15}N values covering all possible sources.

The δ^{15}N *vs.* δ^{13}C plot drawn for the sediment from different density treatments of *Rhizophora mucronata* (Figure 5.2) showed that sediments of all the treatments (including unplanted controls) ranged from -16.41 to -14.58 δ^{13}C and 2.80 to 2.40 δ^{15}N values. Thus, the δ^{15}N range of the treatments could represent material of both seagrass and mangrove origin, while the δ^{13}C range of the treatments is indicative of depleted C of seagrass origin. However, seagrass C can have a wide range of δ^{13}C values and those recorded in this study could be composed of a mix of less depleted seagrass C with mangrove material.

Ideally, the δ^{15}N and δ^{13}C limits of the boxes of different sources on the figure 5.2 should be constructed from isotope readings from the Palakuda experimental site and its terrigenous, mangroves, ocean and seagrass environments. Also, application of mixing models (e.g. isosource) result more accurate sediment carbon signals in coastal areas that receive multiple sources of carbon. Therefore, application of such models to the Palakuda experimental site would result more accurate readings for possible sources of carbon.

However, due to limited resources and time, the above limits (figure 5.2) were decided based on previous publications and therefore the limits of different sources may not be directly applicable to the site studied. The lagoon bed contains *Cymodocea rotundata* and *Enhalus acoroides* (Johnson and Johnstone, 1995) and we have particularly noted highly dense beds of these two types of seagrass close to the experimental site. These seagrass could have been the possible seagrass carbon source for the experimental treatments and a similar situation has been reported from Zanzibar mangroves where the sediments of the fringed area recorded δ^{13}C values of -17.6 ± 0.8‰ due to receiving more δ^{13}C enriched seagrass material. The seagrass material inputs in that case had enriched the sediment δ^{13}C signatures (-17.6‰) close to the range of values from our site (-15.71 to -14.581‰).

Most of the reported %C in mangrove sediment varied between 0.4 to 2.2 (Alongi *et al*. 1993; Kristensen *et al*. 1988, 1991, 1992, 1994; Blackburn *et al*. 1987; Xue *et al*. 2009). However, Middelburg *et al*. (1996) and Wooller *et al*. (2003) reported higher sediment carbon values for Kenyan (3.4 to 11.3 %) and Belize (34%) mangroves. A more recent review by Kristensen (2008) averaged 3.6 to 12 % sediment carbon in world mangroves. Increasing age of the trees and limitation of tidal exchanges increase the sediment carbon (Kristensen 2008; Perry, & Berkeley 2009) and thus the comparatively low sediment carbon in Palakuda planted treatments (0.54 to 0.68%) could also be due to immaturity of the trees and frequent tidal exchanges. The low litter-fall from young trees combined with frequent removal of fallen litter by regular tides is likely to result in the low %sediment carbon values for Palakuda planted plots.

However, comparatively low sediment carbon values (0.1 to 0.2%) have also been reported from 10m high young *Avicennia germinalis* forest in French Guiana (Marchand *et al*. 2003). Although the age of this forest is not mentioned, it indicates that the young mangroves like Palakuda could also have low (<1%) carbon content in their sediments.

The configurations of mangrove forests determine whether the sediment organic carbon is of mangrove, estuarine or marine origin. The mangrove litter may not be a major component of sediment carbon in flow-through ecosystems whereas closed systems largely accumulate local mangrove production into the underlying sediments (Bouillon *et al.*, 2003). The current experimental site counts as a flow-through system as the exchange of water frequently sweeps the entire lagoon bed and therefore most of the leaf litter from the planted mangroves may have been exported to the lagoon water / marine environment with the outgoing tides.. There was no trend of decreasing $\delta^{13}C$ with increasing tree density, despite the significant effect of density on %carbon content. Such a trend would support the hypothesis that the additional sediment carbon at the high density treatments was derived from the mangroves themselves.

The C/N within the plots (including controls) ranged between 7.85-9.32 implying marine organic matter input (C/N= 6 to 9; Jennerjahn and Ittekkot, 1997) to this site (Müller, 1977; Prahl *et al.*, 1980; Krishnamurthy *et al.*, 1986; Uzaki and Ishiwatari, 1986; Meyers, 1994; Jennerjahn and Ittekkot, 1997). However, since the $\delta^{13}C$ (‰) range of all the plots (-16.41, to -14.58) exceeds the $\delta^{13}C$ (‰) range commonly found in marine bottom sediments (-20 to -22; Jennerjahn and Ittekkot, 1997) and marine phytoplankton (-18 to -24: Fry and Sherr 1984), the source of carbon is more likely to be seagrass extensively found adjacent to the plantation site.

The reported sediment silt in Palakuda planted plots ranged from 6.56% (in 6.96 m^{-2}) to 16.11% (in 3.26 m^{-2}) and this range was lower than the sediment silt composition (48 to76%) in Zhangjiang mangrove estuary (Xue *et al*. 2009); but it was more close to the 17% silt reported from Niger Delta sediments (Davies and Abowei, 2009). Also the Palakuda planted plots recorded 79.75 to 83.83 % sand and 0.18 to 0.32% clay in their sediments while the above Niger Delta sediment consisted of comparatively lower sand (57.86 %) and higher clay (24.67%) compositions.

Yang *et al.* (2008) showed an influence of plant density on sediment texture, implying that increasing density results in finer sediments. Such a trend was expected in the current work, given the higher rates of sediment accretion recorded at high densities (Chapter 2). Although the data shown in table 5.6 do show such a general trend, with a mean of 20% silt or smaller at the highest density compared with only 14.5% in the control, significant differences was found only for medium sand out of the ten textural categories. Broader groups of sediment components (clay, total silt, total fine sand, medium sand and total coarse sand) were therefore also compared between treatments using another two-way ANOVA test, although these also showed no significant difference between treatments. This may be a type two error reflecting the small numbers of replicates, and the relatively crude sampling of surface sediments (that would have mixed newly accreted with subsurface material).

5.5 Conclusions

The study found high sediment carbon contents in higher mangrove densities and the isotopic study indicated that is C was not purely of mangrove origin but was apparently influenced by seagrass C. However, a wide isotopic study covering all the possible carbon sources around the Palakuda site is needed for furture confirmation of actual sediment sources. The enhanced sediment accretions in higher planting densities were likely to have increased the sediment carbon indirectly, trapping more fine components (silt) in higher densities although this trend was not significant.

5.6 References

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CHAPTER 6- SUMMARY AND CONCLUSIONS

This section focuses on the overall findings and the conclusions of the current study.

6.1 Sediment accretion and soil elevation in different mangrove densities

The null hypothesis tested at this part of the study was experimentally rejected at the levels of $p<0.05$ and the alternative hypothesis; that the sediment accretion and soil elevation depend on mangrove density was accepted. Therefore the current study discouraged the argument; that increasing shoot or root density to a certain point may cause enhanced erosion from scouring (Spenceley, 1977; Furukawa and Wolanski, 1996) but confirmed the enhanced sedimentation at higher densities as suggested by Morris *et al*. 2002 and Krauss *et al*. 2003. Since the *R. mucronata* produces numerous prop roots (Tomlinson, 1986), the actual effects of its planting density on the sediment accretion should be due to the changes of the above-ground complexity exerted by both stems and the prop root structures. Therefore, studying the changes of the prop root density over time in different planting densities would reflect the changes of aboveground complexity; the controller of the accretion. A test of repeated measure ANOVA showed that the number of prop roots (m^{-2}) varied significantly with time and among plantation densities (Figure 6.1 and Table 6.1). However, there was also a highly significant interaction term between these factors. Tukey`s comparisons showed that the highest tree density had significantly higher number of roots over all the other densities while the 3.26, 1.93 and 0.95 m^{-2} densities were not significantly different from each other.

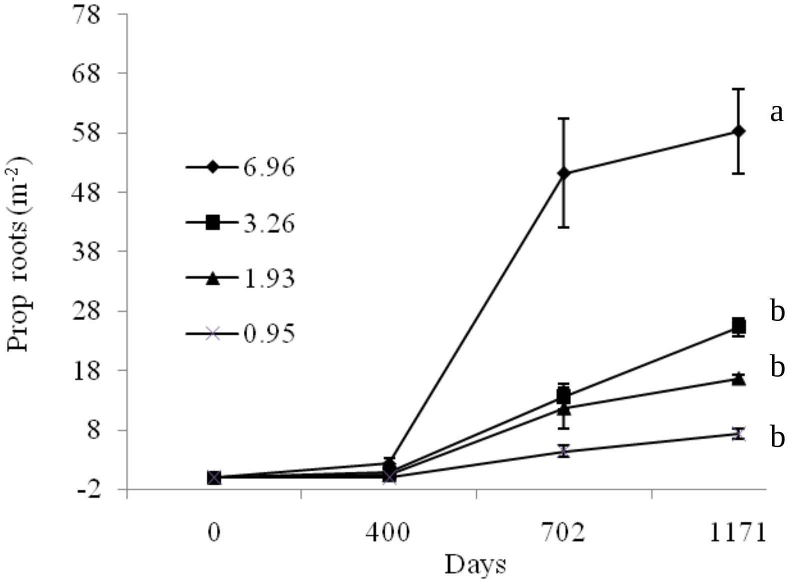


Figure: 6.1. Mean number (±S.E.) of prop roots (m^{-2}) over time in *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Lines represented by different letters identify significantly different mean prop root densities at $\alpha = 0.05$. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95 seedlings m^{-2}

Table: 6.1. Repeated measures ANOVA for Mean prop roots (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka.

Source of variance	DF	MES	F value	P value
Time	2	2177.32	92.75	<0.001
Treatment	3	1937.38	26.88	<0.001
Time × Treatment	6	433.33	18.46	<0.001
Error (Time)	16	23.47		
Error (Treatment)	8	72		
Total	35	4643.52		

Although a clear ranking was observed in the sediment accretion, the prop root density that controlled the sediment accretion did not differ between the 3.26, 1.93 and 0.95 m^{-2} densities. However, the prop root densities of all the tree densities showed a general pattern of increments with time (Figure 6.1) that is essential for enhancing the accretion.

The increased bed roughness in higher mangrove densities slows water movement and facilitates sediment accretion (Quartel *et al.*, 2007; Furukawa and Wolanski, 1996) and under our highest planting density of the current study, the natural sediment accretion of the site (5.7 ± 0.3 mm yr^{-1}; as found in the controls) was elevated to a level of 13.0 ± 1.3 mm yr^{-1}. Ishiwatari *et al.* 1994 suggested that the sediment carbon content may vary with the rate of sedimentation in marine environments and the positive relationship between the sediment carbon and the tree density observed during the current study agreed with this suggestion as the tree density positively correlates with the rate of accretion. Although the accretion rates varied between the tree densities, the accreted materials had the same texture and contained the same source of seagrass carbon implying that the sources of carbon and texture in accreting sediments are independent of the rate of accretion. The below-ground root density increases the soil elevation processes (Krauss *et al.* 2003) and the presence of the highest total root density (4083 ± 536 m^{-2}) in the highest tree was concurrent with the highest soil elevation change (2.8 ± 0.2mm yr^{-1}) observed.

6.2 Mangrove survival and growth under different planting densities

Except for the tree growth, the other parameters (survival, aboveground biomass, belowground biomass and soil N levels) significantly differed between the densities

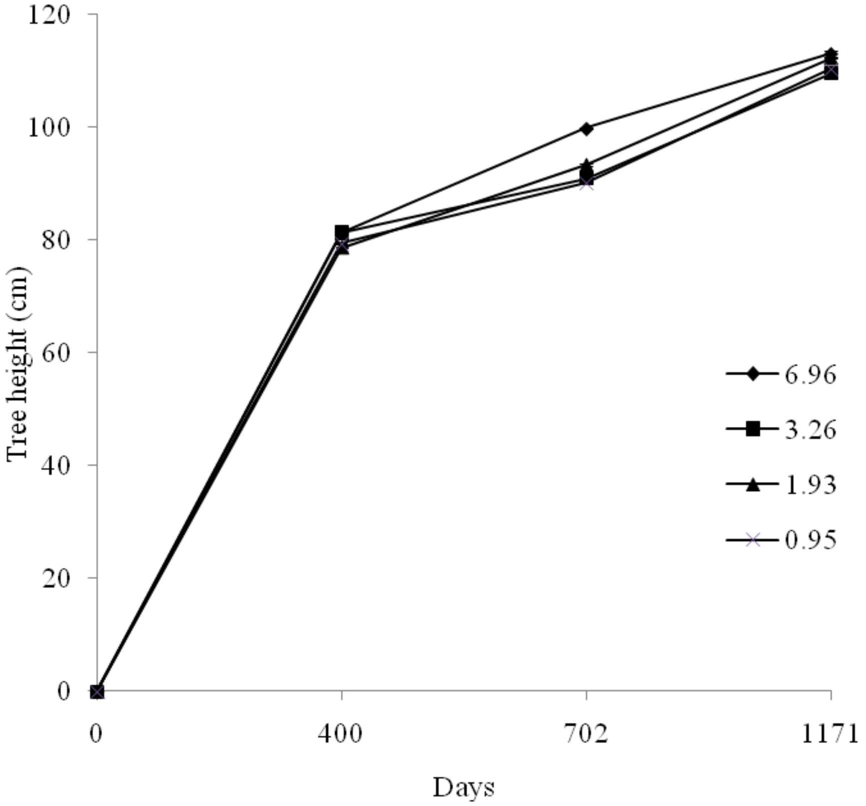
($p<0.05$). Thus, the null hypothesis for the tree growth was accepted whilst for the other parameters, the alternative hypothesis was accepted.

In high density plots, the accreting suspended materials increased the total N and import of N rich materials into mangrove sediments as it has previously been observed in African natural mangroves (Middelburg *et al.*, 1996). Taller trees with enhanced survival have been previously reported for the semi terrestrial tree species; *Terminalia arjuna* at higher planting densities (Srivastava *et al.*, 1999) agreeing with the survival at high density of the current study although the tree height was unaffected compared to the lower densities.

The increased fine root densities are likely to be a strategy for enhancing nutrient absorption against the high nutrient demand by the crowded trees in the highest (6.96 seedlings m^{-2}) tree density. Thus, the high sediment N coupled with these fine roots increased the survival and maintained the growth rate of the high density trees equivalent to those of the low densities.

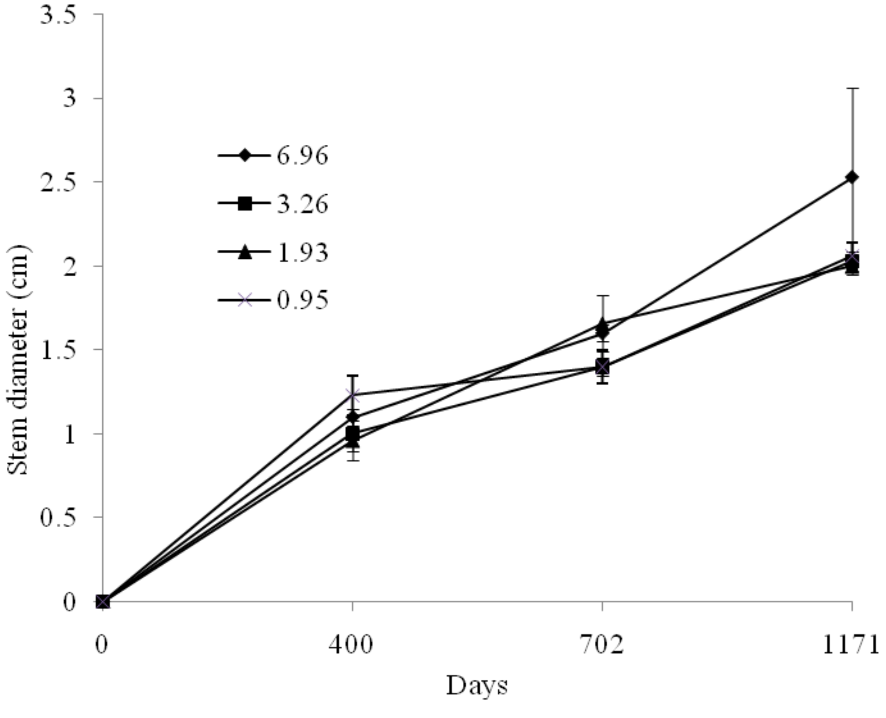
Different parameters of the individual tree growth were not differing among densities and over time (Figure 6.2). Particularly, the tree height showed little deviation among different densities (Figure 6.2a). According to mangrove plantation experiences in Thailand, high density mangroves result in more slender and straight trees when they become nearly 10 years old (Moriizumi *et al.*, 2010) whilst the stem diameters of the trees at higher densities were not smaller than that of the lower densities during the 3 year period of the current study (Figure 6.2b).

a



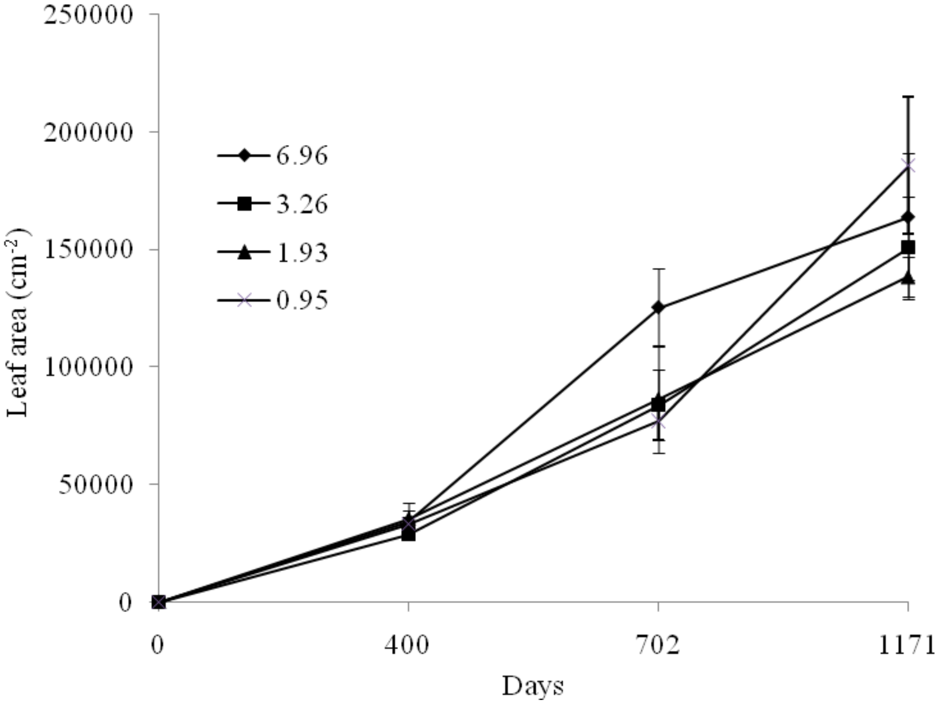
Tree height (cm)
120
100
80
60
40
20
0
0
400
702
1171
Days
6.96
3.26
1.93
0.95

b

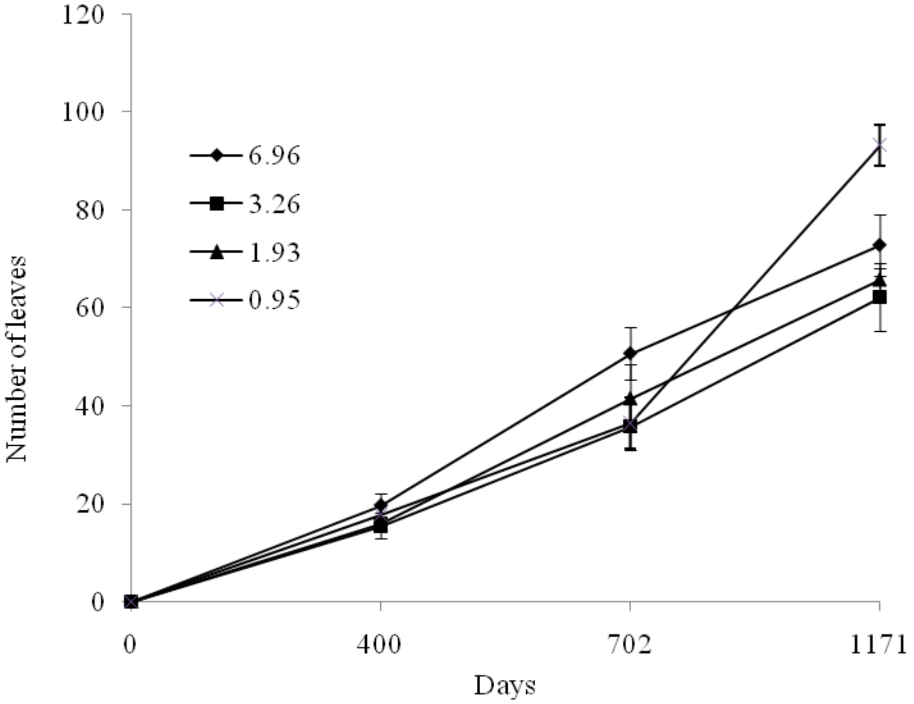


Stem diameter (cm)
3.5
3
2.5
2
1.5
1
0.5
0
0
400
702
1171
Days
6.96
3.26
1.93
0.95

c


250000
200000
150000
100000
50000
0
Leaf area (cm^{-2})
6.96
3.26
1.93
0.95
0
400
702
1171
Days

d


120
100
80
60
40
20
0
Number of leaves
6.96
3.26
1.93
0.95
0
400
702
1171
Days

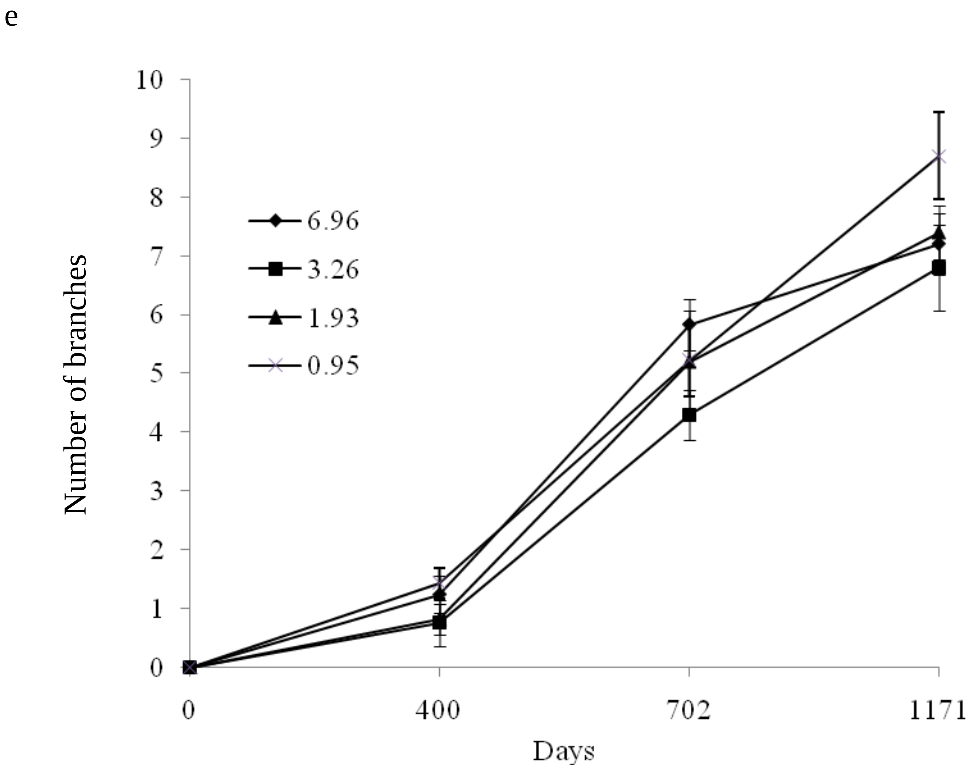


Figure 6.2. Mean (±S.E.) growth parameters (per plant) at different densities of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka. Values next to symbols in the legend represent *R. mucronata* plantation densities of 6.96, 3.26, 1.93, 0.95 seedlings m^{-2}. a= Tree height, b= Stem diameter, c=Leaf area, d=number of leaves, e=number of branches.

The current study found no reductions in growth or survival at increased *Rhizophora mucronata* density; however the optimal planting density may vary between other mangrove species as light requirements are species specific (Imbert *et al*., 2000). Being a more shade-tolerant mangrove group, *Rhizophora* sp (Imbert *et al*. 2000) may have higher growth and survival at higher densities irrespective of possible shading by neighbours trees. However, Kirui *et al*. (2008) reported mean percent survival rates of 42, 56, 71 and 76 in *Avicennia marina* seedlings m^{-2} at the densities of 0.44, 2.25, 4.0 and 8.0, for the first six month of growth. This study supports the findings of the current study, as the increasing seedling density has increased the survival of mangroves. However, it lacks survival data along a time series for further comparisons.

The self thinning reported in older mangroves (e.g. for *Kandelia obovata*; Analuddin *et al.*, 2009) could also be expected in higher densities of the current study with age whilst the extent of thinning for light could be relatively low because *Rhizophora* is more tolerant to shade. The increasing aboveground complexity with age in *R. mucronata* would increase the sediment accretion rates in higher densities and for as long as the resulting accretion rates are capable of importing the adequate nutrients (particularly N) for the crowding trees, any growth reduction may not be observed in the future. In this Palakuda lower intertidal zone, the enhanced N supply by highly accreting sediments might delay any self-thinning of *R. mucronata* at higher densities compared to species in high intertidal areas.

6.3 Mangrove Biomass productions under different planting densities

In order to estimate the accurate total biomass production (belowground + aboveground biomass) up to 1370 days, the tree heights were re-measured and the latest aboveground dry weight (m^{-2}) was calculated for each density. Two-way ANOVA test showed that the total biomass significantly varied between the densities. Tukey`s comparisons showed that the highest tree density (6.96) contains the highest total biomass (m^{-2}) over all the other densities (Table 6.2, 6.3). The 3.26, 1.93 and 0.95 densities were not significantly different from each other ($p>0.05$).

Table: 6.2. Mean (±SE) number of aboveground, belowground and total biomass (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting.

Tree density (m^{-2})	Aboveground biomass (gm^{-2})	Belowground biomass (gm^{-2})	Total biomass (gm^{-2})
6.96	16149±3022	105±6.98	16255±3026
3.26	5526±359	55.4±19.60	5582±376
1.93	4033±778	35.37±2.30	4069±780
0.95	996±185	27.60±5.32	1024±191

Table: 6.3. Two-way ANOVA for the total biomass (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting

Source of variance	DF	SS	MES	F value	P value
Treatment	3	395051589	131683863	17.38	0.001
Block	2	14184253	7092127	0.94	0.443
Error	6	45461592	7576932		
Total	11	454697434			
S = 2753; R-Sq = 90.00%; r-Sq (adj) = 81.67%					

The estimated average productivity of natural mangrove systems is 2500 mg C m^{-2} d^{-1} (Bouillon *et al*., 2002) while the highest (6.96) density resulted 9199 mg d^{-1} rate of above ground dry weight accumulation. The 3.26, 1.93 and 0.95 densities also resulted in aboveground dry weight accumulation rates of 3709, 2253 and 889 mg d^{-1} respectively. This emphasizes the superiority of the higher planting densities (above 3.26 trees m^{-2}) over the natural mangroves in accelerating the absorption of excess atmospheric carbon.

6.4 Changes of Macrofauna under different Mangrove densities

Since the macrofauna community structure was unaffected by the planting density the null hypothesis tested for the macrofauna was accepted at $p>0.05$. Although habitat complexity is reported to change the sediment macrofauna composition in coastal environments (Lindegarth and Hoskin, 2001), there was a clear study gap for testing this concept in intertidal mangroves. The differing tree density under the current study created 4 structural complexities ranging from the zero (0 seedlings m^{-2}) to the highest (6.96 seedlings m^{-2}) and the macrofauna community structure was tested under these differing complexities over time. During a period of 1215 days, the macrofauna density and abundance was found to be independent of the mangrove structural complexity.

Alternatively, the sediment texture which also decides the macrofauna composition (Gray, 1974; Nel *et al.*, 1999, Ysebaert *et al.*, 2003; Ikomi *et al.*, 2005, Atobatele *et al.*, 2005) was found to be unchanged (except for medium sand) among different densities. Frequent removal of leaf litter by tidal activities in this high energy site may have interrupted accumulating particulate organic matter (derived from leaf litter) on sediments and hence no special benefits exsisted for macrofauna under higher tree densities.

The sediments of the higher mangrove densities contained high %sediment C, however it may have been mixed carbon from seagrass and mangroves. These types of mixed carbon may not facilitate typical mangrove fauna which may depend mostly on particulate carbon of mangrove leaf litter. This also could have resulted in the rather similar distribution of surface feeding macrofauna (e.g.: *Cerithidea* sp) between the control and the higher densities. Notably, *Cassidula* sp which is a common gastropod in the Puattalam Lagoon natural mangroves (Pinto 1986) was not recorded from the planted densities implying that organic matter in the sediment of this planted mangrove was still inadequate to sustain some true mangrove macrofauna.

The abundance of crabs in the experimental site and in the natural forest was very low and the sampling area should be increased with special capture techniques for studying the crabs. However, the sample size (5×5×5 cm^3 core) used during the current study for macrofauna sampling was relatively small compare to the plot area (7.2m ×7.2m) and increasing the sampling area and the depth would ensure more accurate results on macrofauna abundance and diversity per unit area. Also, the current study was conducted only for the initial 1215 days mangrove growth and it has not covered the long-term successional changes of macrofauna in planted mangroves. This experiment therefore needs to be continued over the next few years along with increased sampling size to discover the long-term changes of abundance, biomass and diversity of the mangrove macrofauna community.

6.5 Sediment carbon sources under different Mangrove densities

Since the sediment carbon source was unchanged between the densities, the null hypothesis; the sediment carbon source is not affected by mangrove planting density was accepted for this part of the study. The isotope study confirmed the import of suspended estuarine / marine seagrass carbon in to this lower-intertidal mangrove plantation and its significance as organic carbon and nitrogen sources in sediment.

The absence of difference in the sediment carbon source between the planted densities and the unplanted controls indicates that planting mangroves has not supported trapping particular sources of carbon as a matter of changing the structural complexity. Further, the same source of sediment carbon in the highest density and the unplanted controls indicates a continued supply of seagrass carbon in to this site in order that it is not buried by newly accreting high sediment loads in the high densities. The unchanged sediment carbon sources between the treatments (including unplanted controls) indicated planting mangroves or its different tree densities had not supported the settlement of carbon from different sources whilst the increasing density increased the quantity of organic matter accreted into the sediments. This highlights the positive impact of planting mangroves at lower intertidal areas in trapping and sinking marine carbon suspended with tidal water.

Consequently, planting mangrove in Palakuda lower intertidal area imported seagrass carbon in to the planted area while the mangrove litter are exported to the lagoon water from the planted plots and revealing this material exchange between the mangroves and the water column is important in understanding the functioning of planted mangroves.

The carbon stocks in mangrove sediments can be almost entirely of mangroves while in some other mangroves deposited estuarine or marine sediment becomes the dominant source of carbon (Bouillon *et al*., 2003). The current study falls in between these two categories due to the apparent presence of both seagrass and mangrove carbon in the sediment. Trapping seagrass carbon from tidal water signifies the ability of natural mangroves to trap sediments from incoming tides as has been described in a number of previous studies (e.g. Woodroffe 1992; Wolanski *et al.*, 1992; Wolanski 1994; Furukawa *et al.,* 1997; Kathiresan, 2003) however the current study was the first study to show the ability of planted mangroves in trapping marine carbon in lower intertidal areas.

6.6 Conclusions

This study demonstrated how higher mangrove densities enhance the sediment accretion and surface elevation processes that may be crucial in mangrove ecosystem adaptation to sea-level rise. Further, the increasing plant density did not evoke a trade-off with growth and survival of the planted *R. mucronata* trees both at Palakuda and Rekawa sites. Rather, facilitatory effects (mainly due to accumulation of more N under higher accretions) improved the survival at high densities.

The belowground biomass production was significantly higher at high tree densities while the crowding trees accumulated more fine roots within the top soil layers for accelerating nutrient absorption.

The macrofauna community structure was independent of changing tree density possibly due to unchanged sediment texture and or due to absence of adequate leaf litter on the ground. The absence of mangrove carbon as the major source of sediment carbon (chapter 5) also implies export of fallen leaf litter in to lagoon water with outgoing tides.

Thus, the current study implies that the mangrove planters may be able to take advantage of high plantation densities to help mitigate sea-level rise effects by encouraging positive sediment surface elevation. Increasing tree density would not affect low survival or growth reduction during the early growth of mangroves. The current study helps resolve the conflict in mangrove management objectives; enhancing mangrove planting density may result in faster sediment accretion and positive surface elevation increment, but could also lead to higher mortalities from competition. High survival coupled with unaffected early growth in higher densities provides guidance for a maximum per area carbon fixation in tropical coasts and hence efficient land management against increased atmospheric carbon.

However, the short time span of the current research covered only the initial changes of the sediment accretion, soil elevation, tree growth, macrofauna, carbon changes and sediment texture in different mangrove densities relative to the long-term growth and successional changes expected in the mangrove plantations. This highlights the need to continue the current study in terms of understanding the response of the planting density on long-term physical and biological changes in planted mangroves.

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Appendix 1. Distribution of fine roots (Mean ± SE) in different soil depths under different density treatments of *R. mucronata* seedlings; Puttalam Lagoon, Sri Lanka; after 1370 days of planting. L1=0-5cm, L2=5-10cm, L3=10-15cm, L4=15-20cm, L5=20-25cm, L6=25-30cm, L7=30-35cm, L8=35-40cm.

	Mean fine root density (m^{-2}) in different depths							
Tree Density (m^{-2})	L1	L2	L3	L4	L5	L6	L7	L8
6.96	709 ± 102	805 ± 121	753.0 ± 90.4	573.9 ± 64.8	364.1 ± 75.0	298 ± 79.5	177.9 ± 91.5	69.5 ± 20
3.26	439 ± 111	527 ± 106	428 ± 102	362.0 ± 72.3	185 ± 51.3	151 ± 37.8	71.9 ± 29.5	57.7 ± 32
1.93	364 ± 26.5	281.6 ± 11.6	418.4 ± 52.5	301.7 ± 12.5	227.4 ± 50.7	125 ± 29.7	101.3 ± 28.9	66 ± 34.2
0.95	266 ± 136	333.5 ± 83.4	321.7 ± 50.5	249 ± 118	213.3 ± 66.6	87.2 ± 66	47.1 ± 26.2	56.6 ± 30

Apendix 2. Mean belowground dry weight (m^{-2}) at different density treatments of *R. mucronata* seedlings planted in Puttalam Lagoon, Sri Lanka; after 1370 days of planting

Treatment (Seedlings m^{-2})	Belowground dry weight (g m^{-2})
6.96	105.4 ± 6.9
3.26	55.4 ± 19.6
1.93	35.3 ± 2.3
0.95	27.6 ± 5.3