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Mangrove density impacts on surface sediment accretion, belowground biomass and biogeochemistry in Puttalam Lagoon, Sri Lanka

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1 **Impacts of Mangrove Density on Surface Sediment Accretion,**
2 **Belowground Biomass and Biogeochemistry in Puttalam Lagoon, Sri Lanka**

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1 Abstract

2 Understanding the effects of seedling density on sediment accretion, biogeochemistry and
3 belowground biomass in mangrove systems can help explain ecological functioning and inform
4 appropriate planting densities during restoration or climate change mitigation programs. The
5 objectives of this study were to examine: 1) impacts of mangrove seedling density on surface
6 sediment accretion, texture, belowground biomass and biogeochemistry, and 2) origins of the
7 carbon (C) supplied to the mangroves in Palakuda, Puttalam Lagoon, Sri Lanka. *Rhizophora*
8 *mucronata* propagules were planted at densities of 6.96, 3.26, 1.93 and 0.95 seedlings m⁻² along
9 with an unplanted control (0 seedlings m⁻²). The highest seedling density generally had higher
10 sediment accretion rates, finer sediments, higher belowground biomass, greatest number of fine
11 roots and highest concentrations of C and N (and the lowest C/N ratio). Sediment accretion rates,
12 belowground biomass (over 1370 days), and C and N concentrations differed significantly
13 between seedling densities. Fine roots were significantly greater compared to medium and coarse
14 roots across all plantation densities. Sulphur and carbon stable isotopes did not vary significantly
15 between different density treatments. Isotope signatures suggest surface sediment C (to a depth
16 of 1 cm) is not derived predominantly from the trees, but from seagrass adjacent to the site.

17 **Keywords** Mangroves, Sediment nutrients, Accretion, Facilitation, Sri Lanka, Biogeochemistry,
18 Belowground biomass, Stable isotopes, Carbon

19

20

Introduction

21 Mangrove forests trap sediment within their complex aboveground root structures and can
22 influence soil surface elevation; healthy forests with adequate sediment supplies can, therefore,
23 contribute to vertical land building (Wolanski *et al.*, 1992; Furukawa *et al.*, 1997; Krauss *et al.*,
24 2003; Huxham *et al.*, 2010; Kumara *et al.*, 2010). The distribution of different sediment types

1 within mangroves and coastal wetlands depends on local sources of sediment, hydrological
2 conditions, wind and resistance to water flow imposed by the plants (Yang *et al.*, 2008;
3 Ramanathan *et al.*, 2009). The texture and mineralogy of the sediments are closely coupled with
4 local biogeochemical and ecological processes and affect the local nutrient and chemical cycles
5 (Jahnke, 2005; Prasad and Ramanathan, 2009). Hence, mangrove trees influence the nature and
6 amount of sediment present, which in turn may influence the growth of the trees.

7 Mangrove belowground biomass studies can help in understanding nutrient turnover and
8 the potential to store C; however, information on belowground stock is scant (Tamooh *et al.*,
9 2008). Belowground standing stock generally ranges between 0.72 to 30.62 kg m⁻² worldwide
10 (Komiyama *et al.*, 2008; Tamooh *et al.*, 2008) although Cormier *et al.* (2015) report belowground
11 biomass as low as 0.45 to 2.64 kg m⁻² for mangroves in Micronesia. Variations in species
12 diversity, tree density, forest age, level of disturbances and tree growth rates all contribute to this
13 large variance among different mangrove forests. Understanding belowground productivity under
14 different mangrove densities provides the opportunity to broadly illustrate total mangrove
15 productivity (Saintilan, 1997a,b; Komiyama *et al.*, 2000; Alongi and Dixon, 2000; Ong *et al.*,
16 2004; Comley and McGuinness, 2005; Tamooh *et al.*, 2008). Studying processes involving root
17 dynamics is important in understanding forest functions, particularly in mangroves that may invest
18 proportionately large amounts of productivity into their root systems (Saintilan, 1997a,b; McKee
19 *et al.*, 2007). Additionally, fine roots are the principal pathway for nutrient absorption for plants,
20 therefore understanding their distribution in the soil can increase understanding of soil nutrient
21 distribution.

22 In mangrove forests, most of the nutrient pool is stored in the sediment and not in the trees
23 (Alongi, 2009). Despite typically low levels of macronutrients, mangroves manage to sustain

1 very high rates of primary productivity; an average productivity of $0.0025 \text{ kg C m}^{-2} \text{ d}^{-1}$ makes
2 them important components of coastal biogeochemical cycles (Bouillon *et al.*, 2002). This is
3 probably achieved by efficient nutrient cycling and conservation, along with the ability to capture
4 nutrients from outside the system (Alongi, 2009). Allochthonous and autochthonous material is
5 physically, chemically and biologically decomposed in mangrove substrates, with the subsequent
6 organic materials through microbial enrichment processes (Odum and Heald, 1975). Despite this,
7 most mangrove forests experience nutrient limitation, sometimes by phosphorus (Lovelock *et al.*,
8 2007), more often by nitrogen (Alongi, 2009, p38; Reef *et al.*, 2010), and with complex
9 interactions between the two depending in part on location. Studying the physical processes of
10 sediment capture is one important way of understanding controls on growth in mangrove forests,
11 since sediment volume and type may link with nutrient availability, and sediment supply may
12 itself stimulate or repress growth (Lovelock *et al.*, 2007).

13 Sedimentary processes also help to determine the influence of mangroves on coastal
14 geomorphology and erosion. Surface accretion is the height increment of the sediment layer due
15 to gradual deposition of sediment particles and organic material. Surface elevation is the upward
16 movement of sediment due to surface accretion combined with subsurface processes, such as
17 sediment expansion and root growth, discounting for shallow subsidence. These two processes
18 can determine whether the forest floor maintains elevation in relation to sea level, and therefore
19 whether mangroves can help adapt to or mitigate the influence of sea level rise (Gilman *et al.*,
20 2006; McLeod and Salm, 2006; McKee *et al.*, 2007; Gilman *et al.*, 2007, 2008; Krauss *et al.*,
21 2014). Higher plant densities should result in slower current speeds and enhanced accretion,
22 which may contribute to elevation. So exploring the impacts of tree density on surface accretion
23 can increase understanding of coastal geomorphology as well as biogeochemical dynamics. One

1 important applied aspect of this understanding is in coastal restoration and mangrove planting,
2 which is often executed to provide erosion control. Dramatic losses in Sri Lankan mangroves,
3 particularly in the west of the country (Bournazil et al., 2015), combined with the impact of the
4 Asian tsunami, generated extensive mangrove restoration activity within the country (see e.g.
5 IUCN, 2009). Mangrove restoration often fails; Gedan and Silliman (2009) suggest that one
6 reason for this is a failure to anticipate positive plant-plant interactions during early establishment,
7 which may help to overcome establishment thresholds imposed by hydrodynamic forces (Friess et
8 al., 2012). By using a field experiment to examine sedimentary processes during the first two
9 years post-planting the current work may inform the design of mangrove restoration projects.

10 Measuring the ratios of the stable isotopes of carbon in organic material can provide
11 insights into the source of the material. Different taxa of plants synthesize organic carbon (OC)
12 with distinct $^{13}\text{C}/^{12}\text{C}$ values, due to differences in isotopic discrimination by their photosynthetic
13 enzymes and the regulation of diffusion resistance by their stomata (Schweizer *et al.*, 1999; Smith
14 and Epstein, 1971). This C breaks down to detritus and mixes into soil, water or sediments. The
15 movement of sediment may transport this C to different locations, while its original isotopic ratio
16 remains unchanged. Hence, stable isotope ratios provide a means of tracing the origins of C in
17 marine sediments (Fry, 2006; Bouillon *et al.*, 2007; Prasad and Ramanadan, 2009; Otero *et al.*,
18 2000; Bauer *et al.*, 2002). C/N ratios can also be used as indicators for identifying depositional
19 coastal sediment sources (Yu *et al.*, 2010). However, biological alterations or chemical and
20 physical processes in sediments may weaken the capacity of the C/N ratio to distinguish the
21 original source of C (Thornton and McManus, 1994). To overcome this constraint, C/N ratios
22 combined with bulk organic $\delta^{13}\text{C}$ can provide an effective indicator for identifying coastal
23 sediment sources (Yu *et al.*, 2010). For instance, a low C/N ratio coincident with less negative

1 $\delta^{13}\text{C}$ signatures indicates sediments receiving marine or estuarine particulate suspended matter
2 (Bouillon *et al.*, 2003). The present study combines these approaches to understand the likely
3 origin of sedimentary material in experimental mangrove plantations.

4 Whilst tree or root density often correlates with sedimentary characteristics (eg Krauss *et*
5 *al.*, 2003), mangrove systems are highly variable and differences observed in un-manipulated
6 forests may be caused by large numbers of confounding factors. Hence an experimental approach
7 can complement such work by controlling confounders. Here, we use a controlled experiment to
8 study the effects of mangrove tree density on surface sediment texture, accretion, belowground
9 biomass and biogeochemistry. We also examine the origins of the sediment C and N supplied to
10 the mangroves in a study site in the Palakuda, Puttalam Lagoon on the west coast of Sri Lanka.

11 **Materials and Methods**

12 **Study site and experimental design**

13 The study site is at Palakuda, in Puttalam Lagoon, on the west coast of Sri Lanka (Figure
14 1: 8.08° N; 79.73° E). Maximum tidal range in the lagoon is 60 cm with an average of two high
15 tides per day. The surface area of the Puttalam Lagoon is around 400 km² and it is generally very
16 shallow (1-2m), except in the central areas of the lagoon where it can be as deep as 5 m. The
17 lagoon receives two major perennial freshwater inputs from the Kala Oya and Mee Oya Rivers
18 (Figure 1). The salinity of the lagoon varies from oceanic levels (~35 psu) at the northern outlet
19 to 0 psu at river discharge points to hypersaline in the extreme southern portion of the lagoon
20 (Johnson and Johnstone, 1995). Salinity averaged 23 psu at the field site. The experimental site
21 is classified as a flow-through system where the exchange of water repeatedly sweeps the entire
22 lagoon bed.

1 *Rhizophora mucronata* is common in Sri Lankan mangrove forests (Jayatissa *et al.*, 2002),
2 and it occurs naturally at the site. The species grows tall (around 25m), producing considerable
3 numbers of prop roots, and it exhibits vivipary resulting in large stick-like propagules (up to 80
4 cm in length, Duke, 2006) (Kathiresan and Bingham, 2001).

5 In May 2006, fifteen 7.2m × 7.2m plots, arranged in three blocks of five treatments each,
6 with a minimum gap of 1.2 m between plots, were demarcated in the selected mud flat, in an area
7 close to and between patches of natural forest and at the same tidal elevation (Figure 2). The site
8 was chosen after consulting local villagers, who supported mangrove planting here; whilst the
9 area has suffered extensive mangrove deforestation, and there are efforts to restore degraded
10 areas, to our knowledge there were no trees present in the past on these specific experimental
11 plots. Plots were randomly assigned to one of five treatments within each block, which included
12 four planting densities (6.96, 3.26, 1.93 and 0.95 *R. mucronata* seedlings m⁻²) and an unplanted
13 control (0 seedlings m⁻²); hence the highest density treatment was ~ seven times more dense than
14 the lowest and treatments spanned the range of densities found for juveniles in nearby forest.
15 Planting densities equated to 361, 169, 100, 49 and 0 seedlings per treatment. Hence, each
16 treatment was replicated three times within a randomized block design, with blocks included to
17 help account for spatial variability and not to test for hypotheses. For additional details on
18 experimental design, refer to Kumara *et al.* (2010).

19 **Sediment Accretion, Particle Size, Chemical Analysis**

20 At 880 days (approx. 2.4 years) after plantation establishment, four sediment surface
21 scrapes (1 cm depth × 10 × 10 cm area) were taken from random points within each quarter of
22 every plot and combined to give one sample per replicate. Samples were air-dried before being
23 subdivided for carbon, nutrients, particle size and isotopes analyses.

1 Vertical sediment accretion among different densities was measured by setting a mixture
2 of 50% powdered feldspar and 50% white sand over a 30 × 30 cm surface area in the centre of
3 each plot immediately after the trees were planted (Cahoon and Lynch, 1997). Plugs (1 cm² × 5
4 cm deep) were cut out of the sediment in the marker horizon plots and the sediment accretion was
5 measured as the distance from the top of the plug to the feldspar marker horizon with a 1-mm
6 accuracy. Four sediment plugs were measured and averaged to give a single reading for each
7 treatment at each sampling time; marker horizons were replaced every two or three months.
8 Constant re-application of marker horizons creates slightly positive biases in accretion estimates
9 because long-term settling of deposited sediments is not included and some erosion may be
10 inadvertently ignored (Cahoon and Lynch, 1997). However, marker horizons in this study were
11 lost frequently, perhaps because of the regular exchange of water that repeatedly sweeps the entire
12 lagoon bed. Thus, they were re-applied consistently across all treatments. Consequently, overall
13 rates of surface accretion might be slightly higher than long-term averages. Cumulative accretion
14 values and annual accretion rates (mm yr⁻¹) were calculated for each treatment.

15 Small quantities (~1g) of collected sediments were sonicated for 5 minutes using a Cole-
16 Palmer Ultrasonic Homogenizer sonicator on the sediment scrape samples. The % clay
17 (<0.002µm), very fine silt (0.002-0.0032µm), fine silt (0.0032-0.0063µm), medium silt (0.0063-
18 0.02µm), coarse silt (0.02-0.063µm), very fine sand (0.063-125µm), fine sand (125-250µm),
19 medium sand (0.25-0.5mm), coarse sand (0.5–1mm) and very coarse sand (1-2mm) were
20 measured using a Malvern Mastersizer 2000 laser diffraction particle-size analyzer (LDPSA)
21 equipped with a Hydro 2000G.

1 Percent sulphur (S), N and C were measured using a Leco C, S and N analyzer. Sediment
2 pH was determined on a 1:1 ratio w/v of soil and deionized water (Peech, 1965) using a Jenway
3 3150 pH meter.

4 **Belowground Biomass**

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

13 **Isotope Analysis**

14 The sediment scrape samples were oven-dried at 60°C, and then ground to fine powder
15 ($\leq 45\mu\text{m}$) using a Wiley mill. Subsamples for $\delta^{13}\text{C}$ analysis were washed with dilute HCl to
16 remove possible carbonates and were re-dried. Subsamples for $\delta^{15}\text{N}$ were not subjected to this
17 treatment as the acidification affects the $\delta^{15}\text{N}$ values (Pinnegar and Polunin, 1999). Samples for
18 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis were similarly combusted in an elemental analyzer, coupled to an Infra-
19 Red Mass Spectrometry (IRMS) and SP6-350 Visible Spectrophotometer, respectively, via an open
20 split interface. The relative abundance of the heavy and light isotopes of C and N were expressed
21 as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) values by integrated computer analysis. Isotope ratios were calculated
22 using the following equations.

1 Equation 1 was used to determine the C from a specific source in mixed sediments, where

2

$$3 \quad \delta^{13}\text{C} = [(R_{\text{SAMPLE}} / R_{\text{STANDARD}}) - 1] \times 1000 \quad \text{Eq 1}$$

4 $\delta^{13}\text{C}$ = difference measurement made relative to standards (Stable C isotope signatures)

5 R = the ratio of the heavy isotope to the light isotope for the element ($^{13}\text{C} / ^{12}\text{C}$).

6 Equation 2 was to determine the N from a specific source in mixed sediments, where

$$7 \quad \delta^{15}\text{N} = [(R_{\text{SAMPLE}} / R_{\text{STANDARD}}) - 1] \times 1000 \quad \text{Eq 2}$$

8 $\delta^{15}\text{N}$ = difference measurement made relative to standards (Stable N isotope signature)

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

10 **Statistical analysis**

11 Data were analysed for normality and homoscedasticity among residual variances and each
 12 response variable, with the exception of fine root density, was compared among different planting
 13 densities using two-way ANOVA tests with treatments and blocks as factors. In order to explore
 14 the effects of soil depth on fine root density, treatments and soil layers were used as factors in a
 15 two-way ANOVA with the fine root density as the response. The blocking factor in this analysis
 16 was first tested using aggregate data across layers, and then removed because it was non-
 17 significant. Post-hoc multiple range tests were conducted with Bonferroni adjustment (Tukey's
 18 tests). All statistical analyses were carried-out using Minitab, Version 14.20 (Minitab Inc., State
 19 College, PA, USA) or SPSS, Version 13.0 (SPSS Inc., Chicago, IL, USA) statistical packages.

20

Results

21 **Surface Sediment Accretion and Texture in Different Mangrove Densities**

1 Surface sediment accretion rates differed significantly among treatments ($p < 0.01$).
2 Accretion rates increased with tree density (Figure 3). The natural sediment accretion of the site
3 measured on the Control Plots (mean \pm SE of $7.4 \pm 0.3 \text{ mm yr}^{-1}$) was more than doubled to a level
4 of $16.2 \pm 1.3 \text{ mm yr}^{-1}$ under the highest planting density (6.96 m^{-2}). The rate of accretion was
5 significantly higher in the 6.96 density treatment ($p < 0.05$) compared with all the other densities,
6 whilst that in the 3.26 density treatment was significantly higher ($p < 0.05$) (12.7 mm yr^{-2}) than the
7 1.93 (10.6 mm yr^{-2}), 0.95 (8.6 mm yr^{-2}) and control densities (Figure 3).

8 The texture classification of the sediment across the study was medium sand which
9 showed a significant difference across the Palakuda planted plots. The plots recorded 79.75 to
10 83.83% sand and 0.18 to 0.32% clay in their sediments (Table 1). The total proportions of silt,
11 ranged from 19.8% at the highest density (6.96 m^{-2}) to 14.6% in the unplanted controls.

12

13 **Belowground Biomass**

14 **Density of Different Root Types (m^{-2})**

15 The mean number of total roots (m^{-2}) and fine roots (m^{-2}) showed significant differences
16 among the treatments (Figures 4a. c). Tukey's comparisons showed that the highest density
17 treatment (6.96) contained the highest fine and total root densities (m^{-2}) over the lowest seedling
18 density (0.95). The highest seedling density had $3751 \pm 426 \text{ m}^{-2}$ fine roots, 2.4 times higher than
19 that of the lowest tree density ($1574 \pm 359 \text{ m}^{-2}$). Thus, increasing the density by approximately
20 7.3 times increased the fine root density by 2.4 times. Regardless of the significant increase in
21 fine roots, none of the tree densities showed significant differences for medium or coarse roots
22 which could be due to these roots having more of a structural/support function.

23

1 **Fine Root Density (m^{-2}) at Different Soil Depths**

2 The mean fine root density (m^{-2}) significantly varied among the plantation densities
 3 (Figure 4b) in the 5-10 cm layer. The mean fine root density of the 6.96 seedling m^{-2} plantation
 4 density ($805 \pm 121 \text{ m}^{-2}$) within the 5-10 cm layer was significantly higher (Tukey test; $p < 0.05$)
 5 than fine root densities of the 1.93 (281.6 ± 11.6) and 0.95 (333.5 ± 83.4) plantation densities,
 6 while the fine root density of the 3.26 seedling m^{-2} plantation density did not differ from the
 7 densest seedling plots. The 3.26, 1.93 and 0.95 seedling m^{-2} plantation densities were not
 8 different from each other within this 5-10cm layer. The mean fine roots density (m^{-2}) of different
 9 plantation densities significantly differed in the 10-15cm layer where the 6.96 seedling m^{-2}
 10 plantation density ($753 \pm 90.4 \text{ m}^{-2}$) was significantly higher ($p < 0.05$) than those of the 0.95
 11 seedling m^{-2} plantation density (321.7 ± 50.5). All tree densities showed a general pattern of
 12 reduction of fine root densities with depth.

13

14 **Belowground Dry Biomass**

15 The total belowground biomass (g m^{-2}) significantly varied among the treatments. The
 16 highest seedling density (6.96 m^{-2}) contained the highest belowground dry weight (105.41 ± 6.98
 17 g m^{-2} ; Figure 4c), while the other densities did not significantly differ ($p > 0.05$). The total
 18 belowground biomass was $27.6 \pm 5.3 \text{ g m}^{-2}$ in the 0.95 m^{-2} plot, $35.57 \pm 2.3 \text{ g m}^{-2}$ in the 1.93 m^{-2}
 19 plot, and $55.5 \pm 19.6 \text{ g m}^{-2}$ in the 3.26 m^{-2} plot.

20 **Carbon, Nitrogen, Sulphur and pH**

21 The percentage of total C in the surface sediment varied significantly among the
 22 treatments (Figure 5). For the highest density of 6.96 seedlings m^{-2} , the % C (mean \pm SE) was
 23 $0.68 (\pm 0.04)$, while the C values for 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were $0.55 (\pm 0.08)$, 0.53

1 (± 0.05), 0.54 (± 0.04), and 0.46 (± 0.05), respectively. Tukey`s comparisons showed a
2 significantly higher C in the highest (6.96 seedlings m^{-2}) seedling density, compared to the
3 unplanted controls. There were no significant differences in the sediment C among the other
4 treatments.

5 Sediment N also varied significantly ($p < 0.05$) among plantation densities; the % N in
6 surface sediments in the 6.96 m^{-2} density treatment was significantly higher ($p < 0.05$) compared
7 with the other treatments (which showed no significant differences among themselves; Figure 5).
8 For the highest density of 6.96 seedlings m^{-2} , the % N (mean \pm SE) was 0.08(± 0.007), while the
9 N values for 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were 0.06 (± 0.009), 0.007 (± 0.003), 0.07 (\pm
10 0.006), and 0.05 (± 0.001), respectively.

11 C/N ratios for the sediments showed no significant differences among planted treatments
12 but differed significantly between the planted treatments and the control; the latter showed the
13 highest mean ratio which was significantly greater than 1.93 and 0.95 densities. C/N ratios for
14 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 (\pm
15 0.51), and 9.32 (± 0.72), respectively (Table 2).

16 Sulphur did not vary significantly among the different density treatments (Figure 5)
17 indicating an adequate supply for the seedlings irrespective of the higher demand in the higher
18 seedling densities. For the highest density of 6.96 seedlings m^{-2} , the % S (mean \pm SE) was 0.12 (\pm
19 0.02), while the S values for 3.26, 1.93, 0.95 and 0 seedlings m^{-2} were 0.09 (± 0.00), 0.11 (± 0.01),
20 0.11 (± 0.01), and 0.07 (± 0.00), respectively. Levels of S were not significantly different
21 between the unplanted controls and the planted plots. This implies that seedling growth is
22 unlikely to be limited by macronutrients needed for normal development in plants.

1 Sediment pH ranged from 7.6-7.8 among the densities (Table 2) with no significant
2 differences.

3

4 **Stable Isotopes**

5 The mean $\delta^{13}\text{C}$ values for sediment taken from the 6.96, 3.26, 1.93, 0.95 and 0 seedlings
6 m^{-2} treatments did not differ significantly (Table 2). The ‰ (\pm SE) $\delta^{13}\text{C}$ values for 6.96, 3.26,
7 1.93, 0.95 and 0 seedlings m^{-2} were $-16.13 (\pm 0.95)$, $-15.85 (\pm 0.97)$, $-15.71 (\pm 0.40)$, $-16.41 (\pm$
8 $0.14)$, and $-14.58 (\pm 0.30)$, respectively. The absence of significant differences in isotopic
9 signatures suggests that much of this soil surface C was allochthonous and arrived with the
10 accreting sediment.

11 There were no significant differences among mangrove density in $\delta^{15}\text{N}$ values in
12 sediments (Table 2). The ‰ (\pm SE) $\delta^{15}\text{N}$ values for 6.96, 3.26, 1.93, 0.95 and 0 seedlings m^{-2}
13 were $2.80 (\pm 0.13)$, $2.73 (\pm 0.29)$, $2.40 (\pm 0.24)$, $2.41 (\pm 0.22)$, and $2.49 (\pm 0.11)$, respectively.

14

15

15 **Discussion**

16 **Higher Mangrove Densities Increase Sediment Accretion**

17 The increased drag coefficient at higher mangrove densities slows water movement and
18 facilitates sediment accretion (Quartel *et al.*, 2007; Furukawa and Wolanski, 1996). Ambient
19 sediment accretion measured on the control plots (mean \pm SE of $7.4 \pm 0.3 \text{ mm yr}^{-1}$) was less than
20 half the $16.2 \pm 1.3 \text{ mm yr}^{-1}$ recorded under the highest planting density (6.96 m^{-2}). Greater
21 plantation densities also help prevent erosion of deposited sediments by slowing water velocities,
22 and perhaps by promoting greater fine root production to facilitate sediment retention (Krauss *et*

1 *al.*, 2003; Lovelock *et al.*, 2007). Friess *et al.* (2012) suggest that reduced water speeds and fast
2 early root growth (which ensures rapid stabilisation) may be key elements in determining
3 successful colonisation of mangroves in new sites. They discuss the importance of natural
4 variations in these variables, in particular the existence of unusually calm hydrodynamic periods
5 and of fast root growth in pioneer species. Our results suggest that restoration efforts may benefit
6 from deliberate manipulation of these variables by using high densities, slowing water speeds and
7 encouraging sedimentation, which in turn can stimulate root production.

8 The sediment size classification was medium sand for the site with total sand ranging from
9 79.75 to 83.83 %. Silt provided a smaller fraction of the sediment here than recorded in some
10 comparable studies, such as the 48 to 76% in the Zhangjiang mangrove estuary of China (Xue *et*
11 *al.* 2009), but was similar to the 17% silt-size fraction reported from Niger Delta sediments
12 (Davies and Abowei, 2009). Sediments with weak texture (dominated by sand) are eroded more
13 easily compared with sediments dominated by clay, which are more resistant to coastal erosion
14 (Yang *et al.* 2008). Sediments with finer textures also usually have higher nutrient concentrations,
15 partly because of their greater ability to bind nutrients onto particle surfaces and within interstitial
16 spaces. The Palakuda planted plots had only 0.18 to 0.32% clay in their sediments. In addition to
17 influencing sediment accretion (Kumara *et al.*, 2010), the grain-size distributions of tidal wetland
18 sediments impact the nutrient, OM and water contents of sediments (Lovelock *et al.*, 2007), and
19 determine local biogeochemistry (Dylan and Dahlgren, 2005; Zhou *et al.*, 2007).

20

21 **Impacts of Seedling Density on Roots and Belowground Biomass**

22 There were significantly higher amounts of fine roots in all planted plots compared to
23 medium and coarse roots. Fine roots are more efficient in absorbing nutrients than coarser roots

1 as they dramatically increase the surface area for absorption. In the highest seedling density,
2 nutrient demands from the soil should be higher, and therefore, the seedlings in that density need a
3 special strategy to accelerate the rates of nutrient absorption. Regardless of the significant
4 increase in fine roots, none of the tree densities showed significant differences ($p < 0.05$) for
5 medium or coarse roots because these roots may have more of a structural/support role. This
6 finding has also been reported in other studies on mangroves in Micronesia (Cormier *et al.*, 2015)
7 and the Everglades in Florida, USA (Castaneda-Moya *et al.*, 2011).

8 The general trend of reduction of fine root density with depth, except at the 5-10cm depth,
9 shown by all the seedling plantation densities (Figure 4b) also indicated the importance of the
10 upper soil layers in nutrient absorption. The frequent wave and tidal activities are likely to disturb
11 the nutrient absorption in the upper most 0-5cm layer and this could be the reason for fewer fine
12 roots at the surface, compared to the underneath 5-10cm region which is more stable from
13 disturbances.

14 The belowground dry weight did not increase proportionally with the increasing seedling
15 density, which was the case with the aboveground biomass production at this site (Kumara *et al.*,
16 2010). The reason for this is not obvious and uneven growth of roots in the intermediate seedling
17 plantation densities ($3.26, 1.93$ and 0.95m^{-2}) or low sample size could be the cause; however,
18 further research is needed to understand the actual reasons for this disproportionate growth.
19 Reported mangrove belowground biomass ranges between 0.45 to 30.62 kg dry matter m^{-2}
20 (Komiyama *et al.*, 2008; Tamooh *et al.*, 2008; Cormier *et al.*, 2015); the belowground biomass in
21 this study, even in the highest seedling density (0.11 ± 6.98 kg dry matter m^{-2}), did not reach even
22 the lowest limit of this range (probably because of the young age of the mangroves in the study),

1 suggesting that the rhizosphere was not saturated with roots and that competitive processes were
2 not limiting root growth even at high density.

3

4 **Impacts of Seedling Density on Biogeochemical Variables**

5 The surface sediment values of C and N recorded in this study were low overall and
6 showed significant differences among treatments. The enhanced sediment C and N values
7 recorded in the highest density treatment were probably caused by greater accretion rates at higher
8 planting densities. A global review by Kristensen (2008) reported average sediment C values of
9 3.6 to 12 % in mangroves. At 0.54 to 0.68%, the current site has unusually low values of C
10 (although sites with values down to 0.1% have been reported, e.g. Marchand *et al.*, 2003).

11 Increasing age of the trees and limitation of tidal exchanges increase the sediment C (Kristensen,
12 2008; Perry and Berkeley, 2009; Osland *et al.*, 2012), and thus the comparatively low sediment C
13 in Palakuda planted treatments is probably due to the immaturity of the trees and regular tidal
14 exchange.

15 Seedling growth and survival was better at high than low densities, suggesting a
16 facilitative effect between trees (Kumara *et al.*, 2010). This is likely to have resulted from higher
17 N supply from the accreting sediments at higher densities. An enhanced supply of N brought
18 about by increased sediment accretion is likely to have compensated for the potential competition
19 for N under increased seedling densities. Similar positive effects of N supply linked to
20 sedimentation have been recorded elsewhere, although the mechanisms that promote growth may
21 involve stimulation by sedimentation itself as well as through associated nutrient input (Lovelock
22 *et al.*, 2007).

1 Salinity can lead to a deficiency of nutrients such as S (Diop *et al.*, 2002). S can also be
2 used as a marker for anoxia. The lack of any differences in S between treatments suggests no
3 differences in oxygen availability or limitation by S. Frequent tidal exchanges at the site and the
4 high rates of sediment accretion might have resulted in this supply. Sediment pH ranged from
5 7.6-7.8 among the densities (Table 2) with no significant differences. Most mangrove sediments
6 are acidic because of anaerobic decomposition of organic matter (OM) (Alongi, 2009; p90); this
7 relatively high pH reflects the low OC content found.

8

9 **Isotopic Analysis Reveal Seagrass as a Sediment Carbon Source**

10 Although the accretion rates varied among the seedling densities, the accreted materials
11 had the same texture and the isotope results suggest they contained the same source C implying
12 that the sources (rather than amounts) of C and texture in accreting sediments are independent of
13 the rate of accretion.

14 Carbon derived from mangrove litter and exudates (Prasad and Ramanadan, 2009) and fine
15 roots typically has $\delta^{13}\text{C}$ values of around -29.75 to -27.64. Therefore, sediments with values close
16 to these are likely to be dominated by mangrove C inputs, whilst less depleted signatures such as
17 $\delta^{13}\text{C} = -22.4$ imply higher marine influence (Bouillon *et al.*, 2007). The C isotope values here
18 suggest that marine sources dominated the C pool in the experimental plots.

19 Mangrove sediments undergo various nitrogenous processes such as mineralization,
20 nitrification, volatilization, denitrification and isotope fractionation and produce a wide range of
21 $\delta^{15}\text{N}$ signatures (typically 0 to ~13) (Voss *et al.*, 2005; Hu *et al.*, 2006). For constraining a wide
22 range of C sources in coastal sediments, the classic $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ plot is used in this study because

1 the $\delta^{13}\text{C}$ axis ranges from terrestrial (more negative) to marine (higher) values (Bouillon *et al.*,
2 2000; Dehairs *et al.*, 2000; Carreira *et al.*, 2002; Barros *et al.*, 2010), while the $\delta^{15}\text{N}$ axis also
3 represents a sufficient range of $\delta^{15}\text{N}$ values covering all possible sources. Ideally, the $\delta^{15}\text{N}$ and
4 $\delta^{13}\text{C}$ limits of the boxes of different sources in Figure 6 would be constructed from isotope
5 readings from the Palakuda experimental site and its terrigenous, mangrove, ocean and seagrass
6 environments; instead the data here are drawn from the literature for other, similar sites. The
7 lagoon bed contains the seagrasses, *Cymodocea rotundata* and *Enhalus acoroides* (Johnson and
8 Johnstone, 1995), and we have observed dense beds of these two types of seagrass close to the
9 experimental site. These seagrasses are a possible C source for the experimental treatments; a
10 similar situation has been reported from Zanzibar mangroves where the sediments of the fringed
11 area recorded ^{13}C values of $-17.6 \pm 0.8\text{‰}$ due to receiving more $\delta^{13}\text{C}$ enriched seagrass material.
12 The seagrass material inputs in that case had enriched the sediment $\delta^{13}\text{C}$ signatures (-17.6‰)
13 close to the range of values from our site (-15.71 to -14.581‰) (Muzuka and Shunula, 2006).

14 A C/N ratio of between 7.85-9.32 implies a marine organic matter input (C/N= 6 to 9) to
15 this site (Jennerjahn and Ittekkot, 1997). Osland *et al.* (2012) also found that there was a positive
16 developmental trajectory that indicates a closely associated and fast plant-soil change where the
17 development of mangrove forest occurs simultaneously with upper sediment layer peat
18 development, N and C accumulation and changes in bulk density. The location and configuration
19 of mangrove forests determine whether the sediment OC is of mangrove, estuarine or marine
20 origin. The mangrove litter may not be a major component of sediment C in flow-through
21 ecosystems, whereas closed systems largely accumulate local mangrove production into the
22 underlying sediments (Bouillon *et al.*, 2003). The current experimental site is a flow-through
23 system as water frequently sweeps the entire lagoon bed, and therefore, most of the leaf litter from

1 these relatively small planted plots is probably exported to the lagoon water / marine environment
2 with the outgoing tides.

3 **Conclusions**

4 The density of mangroves affected the granulometry and chemistry of accreting sediment
5 and the belowground biomass of the trees. The highest seedling density had the highest
6 belowground biomass and the greatest numbers of fine roots for efficient absorption of nutrients,
7 with the highest number of total roots present at soil depths of 5-10 cm. Higher seedling densities
8 had higher levels of sediment accretion and associated nutrient content. The C/N ratio for
9 sediments in planted treatments differed significantly from the unplanted control, reflecting the
10 enhanced N found in planted plots. The $\delta^{15}\text{N}$ range of the treatments could represent material of
11 both seagrass and mangrove origin, while the $\delta^{13}\text{C}$ range of the treatments is indicative of
12 enriched C of seagrass origin. Sediments from all the treatments (including unplanted controls)
13 ranged from -16.41 to -14.58 for $\delta^{13}\text{C}$ and 2.80 to 2.40 for $\delta^{15}\text{N}$ with no significant differences in
14 the ‰ $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in sediments among different mangrove densities; taking these isotopic
15 results together suggests that most C in the plots was derived from allochthonous sources.
16 Sediment %N and %C differed significantly among densities, which suggests one potential causal
17 mechanism for the facilitatory effects on growth previously observed: high densities of plants
18 potentially contribute to the accretion of greater amounts of nutrient-rich sediment, which may be
19 particularly important at this site which has low levels of C, N and silt in the ambient sediment.
20 The current study involved a single sampling of sediment after 880 days of planting, and hence,
21 the conclusions are mostly applicable for the initial growth of the mangroves only. A more
22 detailed study with samplings at different growth stages of these experimental plots is required to
23 understand the long-term dynamics of the measured sediment parameters.

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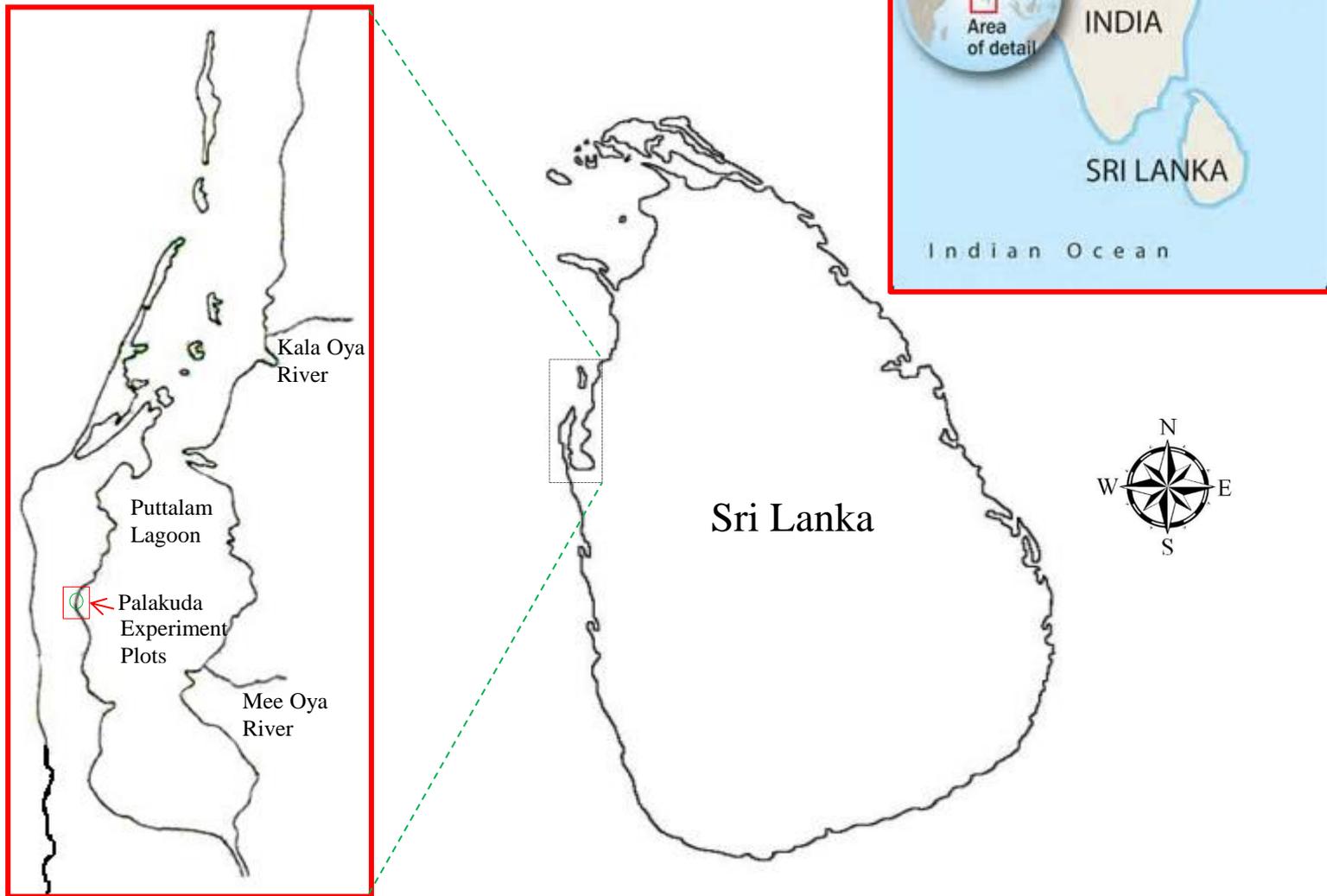


Figure 1. Location of Palakuda within Puttalam Lagoon in Sri Lanka where the experimental plots were established.

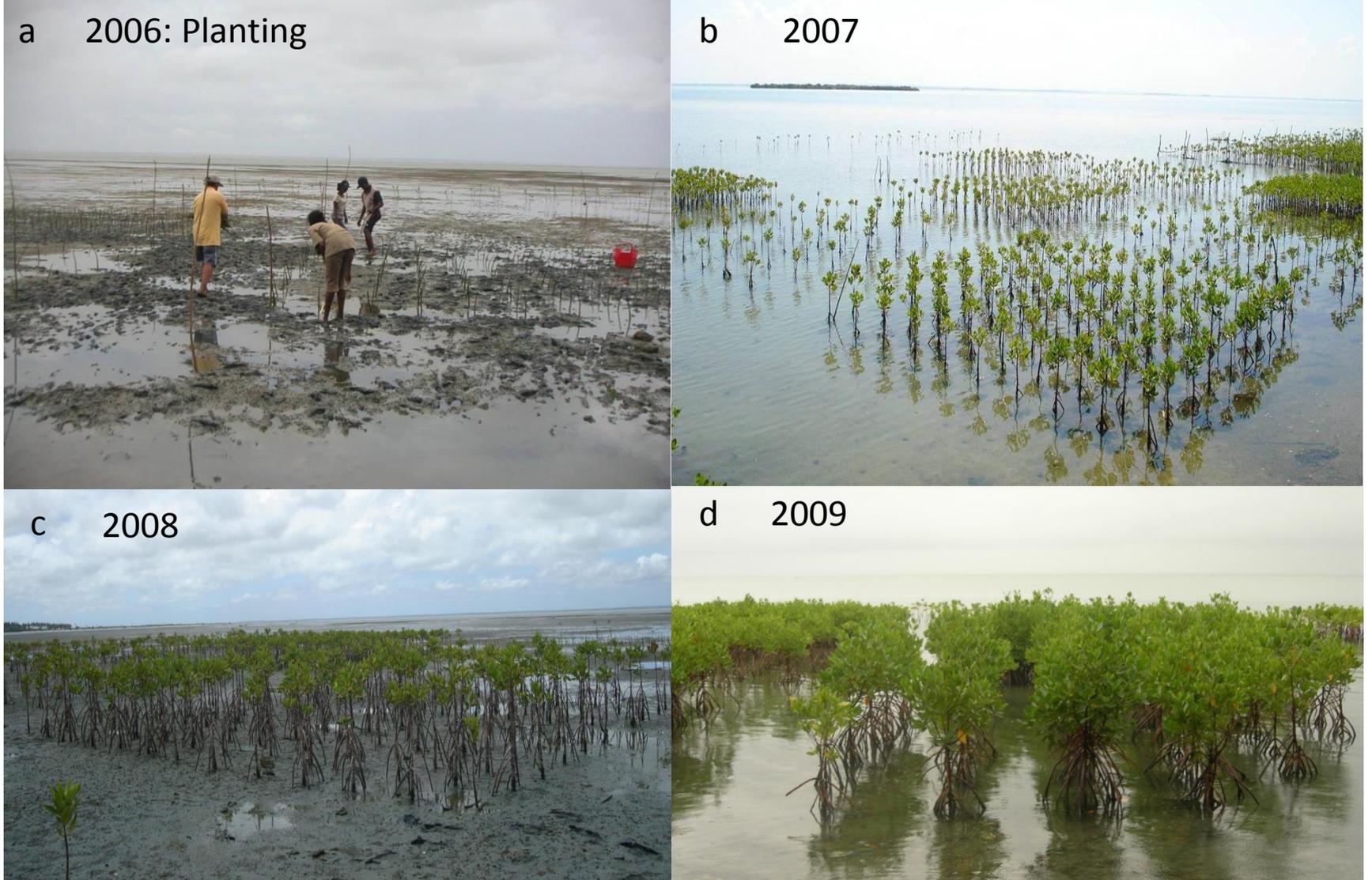


Figure 2. Palakuda experimental site, Puttalam Lagoon, Sri Lanka. A) Planting of *R. mucronata* seedlings in 2006, and tree growth in plots in b) 2007, c) 2008, and d) 2009.

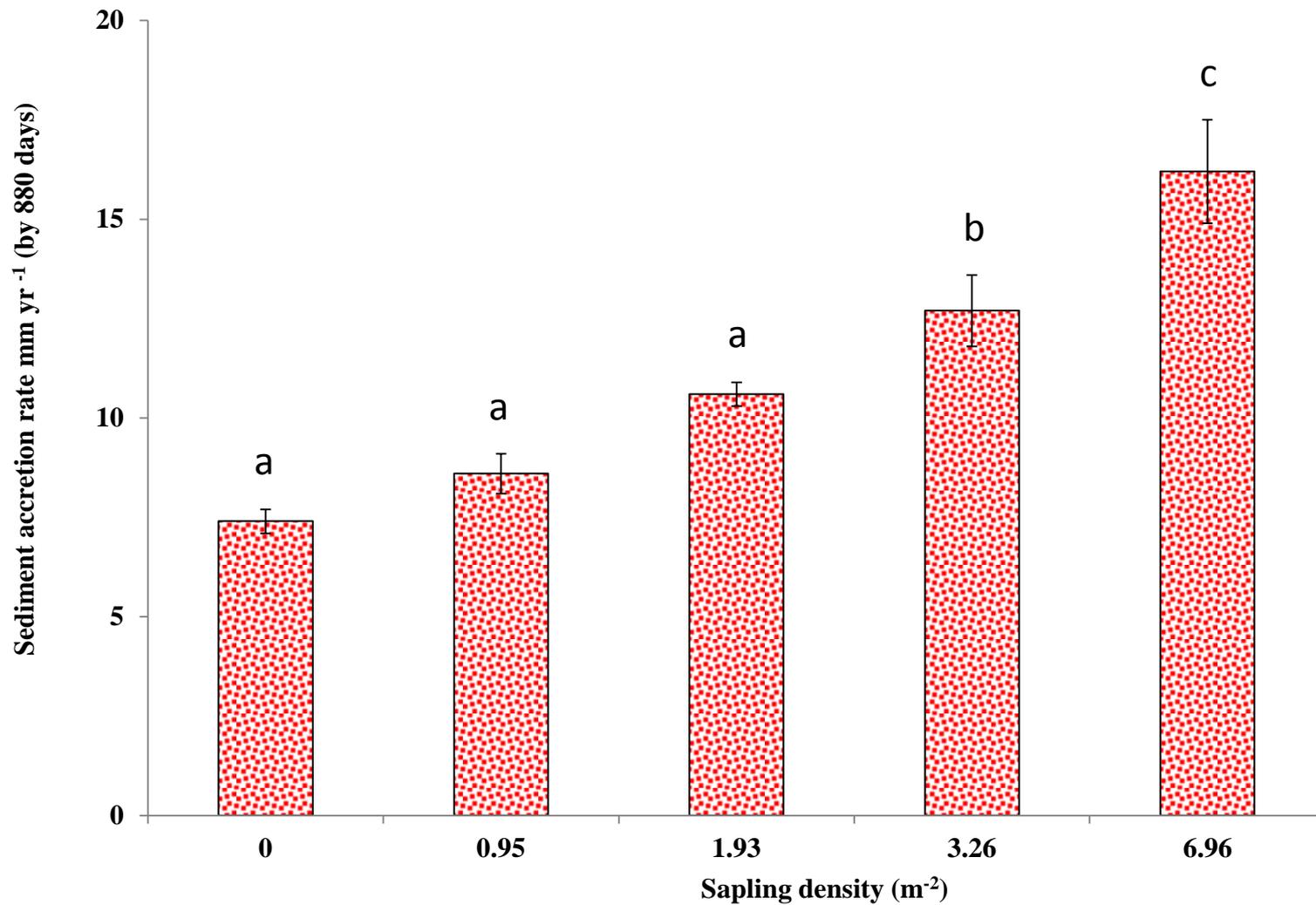


Figure 3. Mean (\pm SE) accretion rates over 880 days. Letters show statistically distinct means.

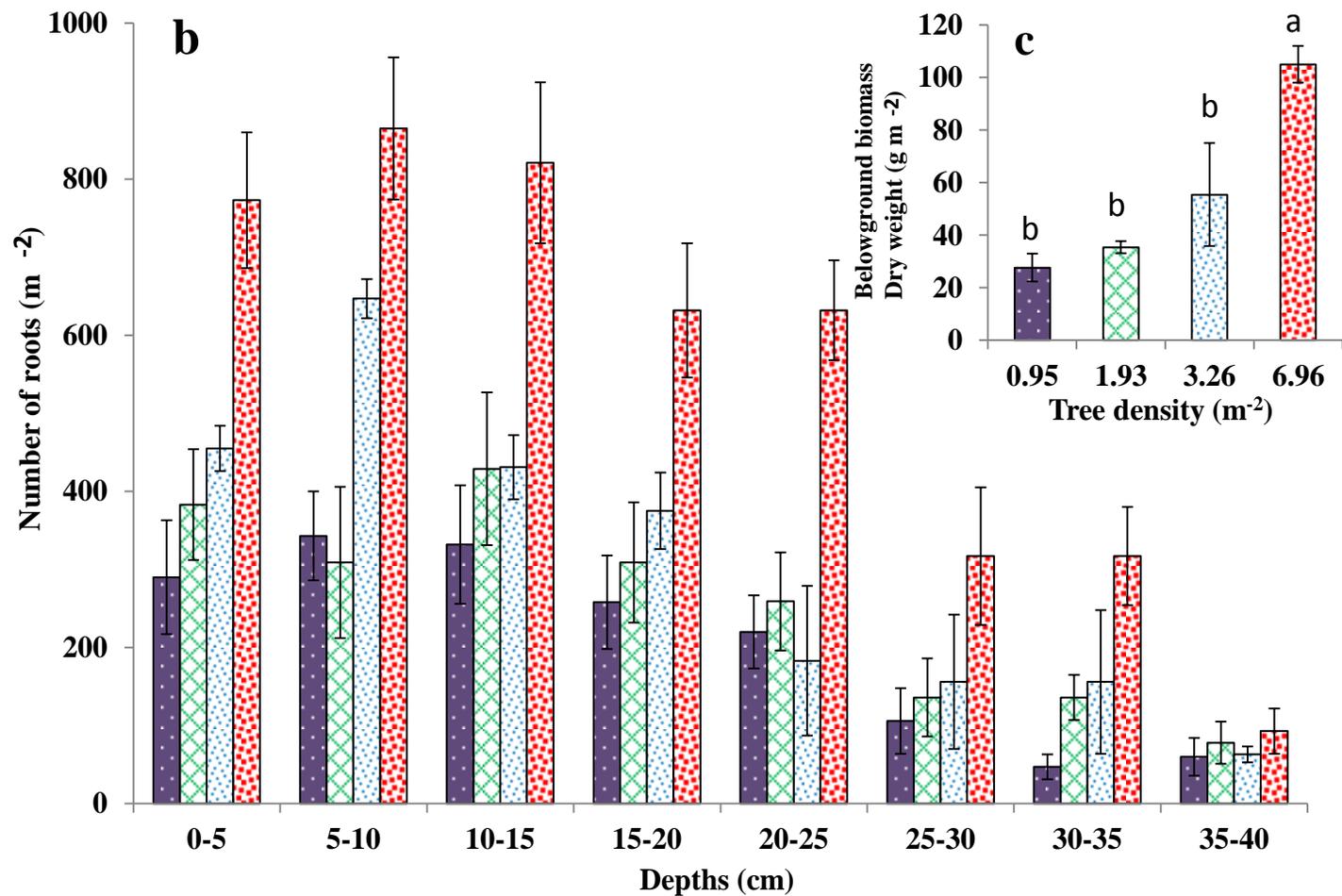
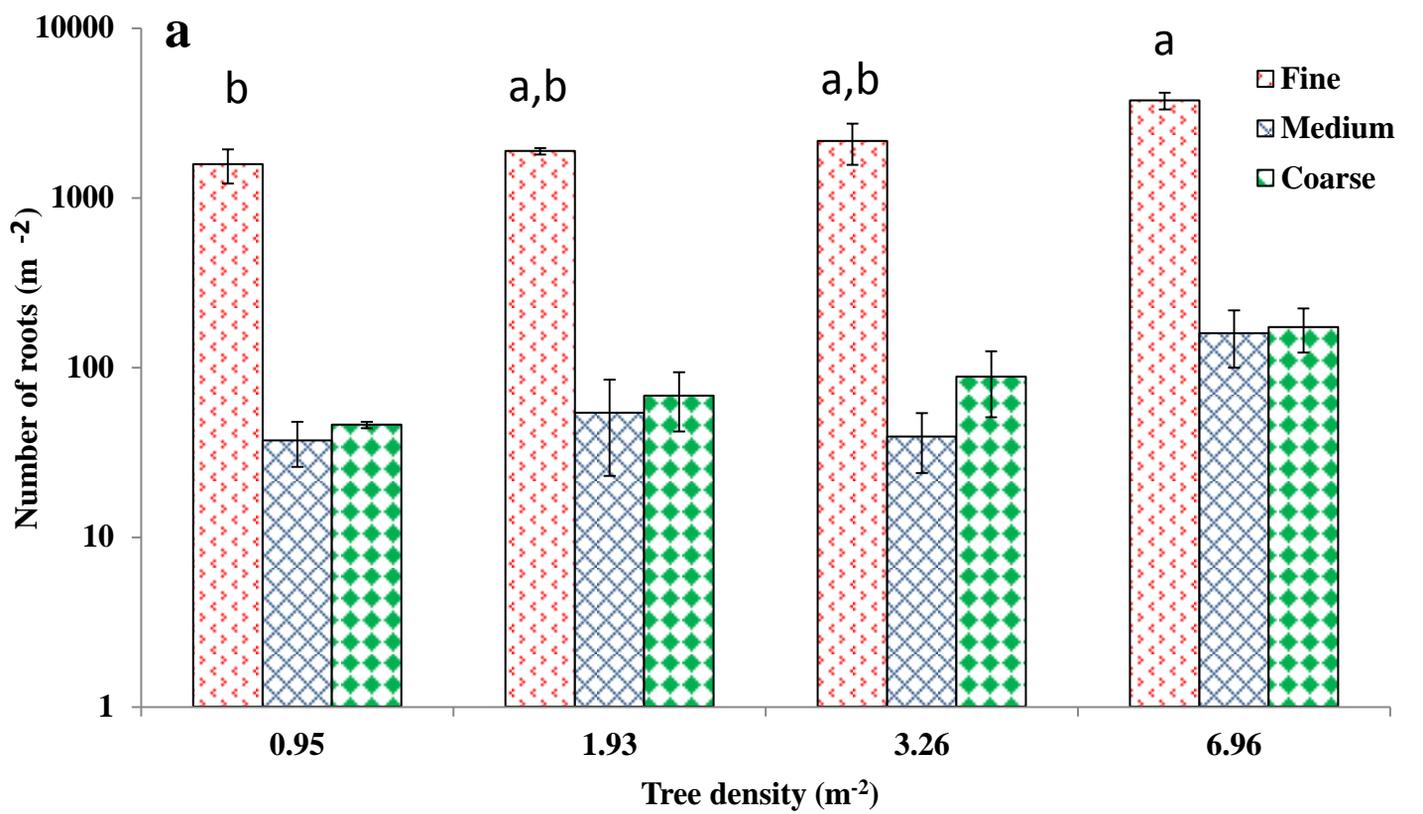


Figure 4. Belowground a) different size classes of roots, b) root growth, and c) biomass dry weights (\pm S.E.) per planting densities of *R. mucronata* seedlings at different density treatments.

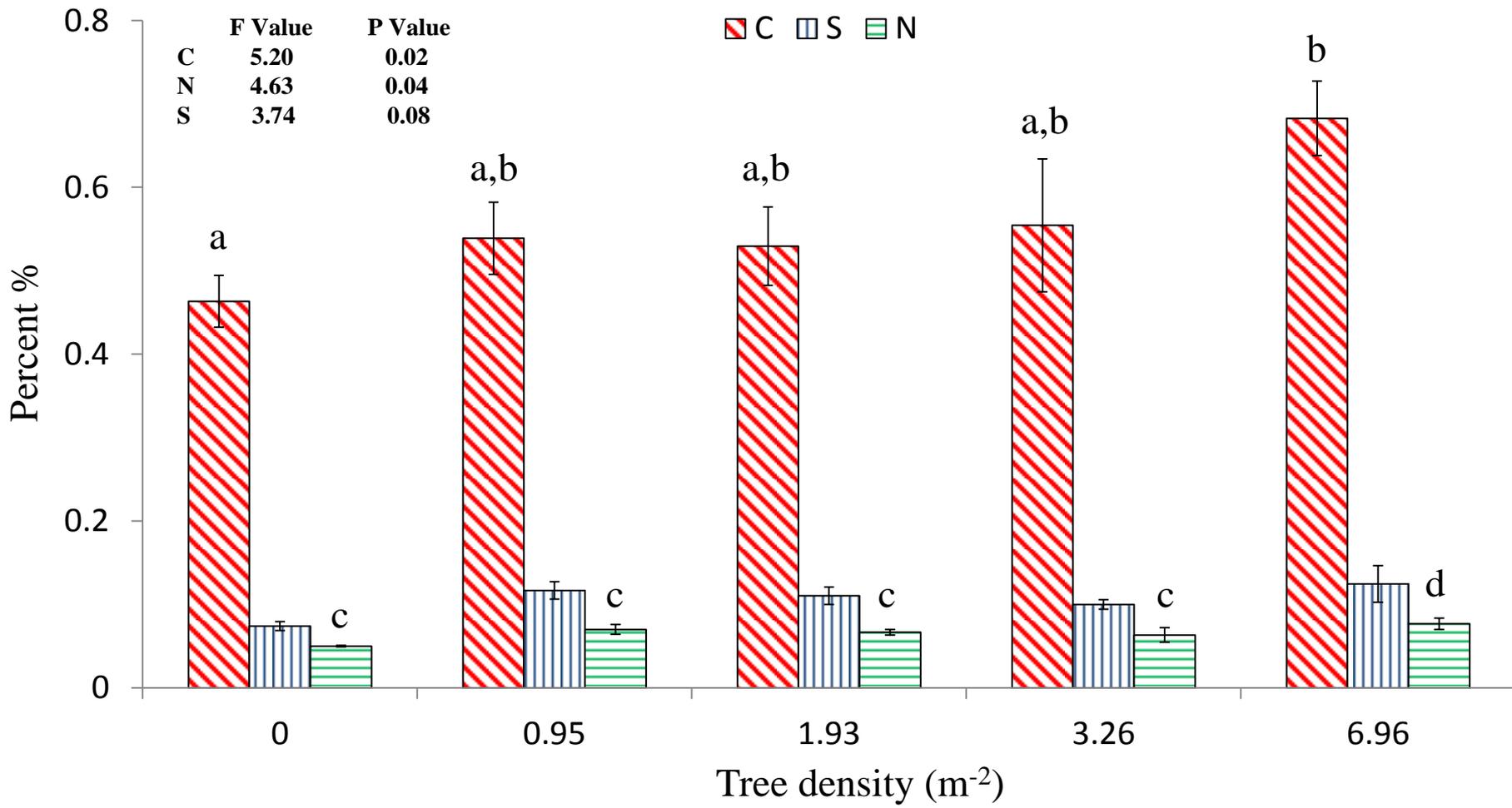


Figure 5. Percent (means ± SE) carbon, sulphur, and nitrogen for the different tree densities in the study. Letters show statistically distinct means. The p and f values obtained from Two-way ANOVA test.

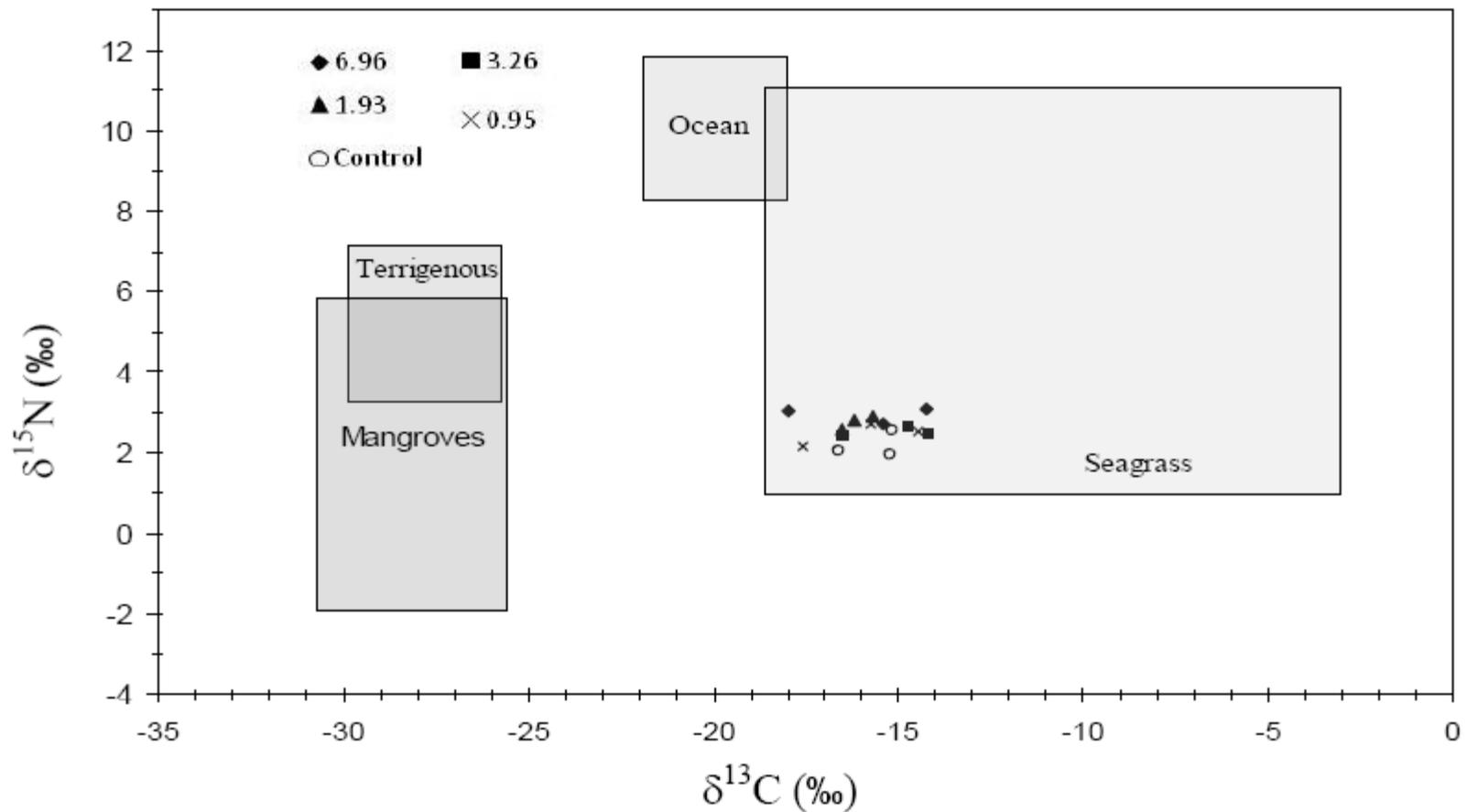


Figure 6. Position of different *R. mucronata* density treatments with $\delta^{15}\text{N}$ vs $\delta^{13}\text{C}$ plot of potential sources. Different symbols indicated different treatments. Sources used for producing the limits of the shaded boxes: McMillan, 1980; Fontugne and Duplessy, 1981; Fry and Sherr, 1984; Meyers, 1984; Macia, 1995; Hemminga and Mateo, 1996; Jennerjahn and Ittekkot, 1997; Margaillier *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.