



Below-ground root yield and distribution in natural and replanted mangrove forests at Gazi bay, Kenya

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ARTICLE INFO

Article history:

Received 14 March 2008

Received in revised form 8 June 2008

Accepted 23 June 2008

Keywords:

Mangrove

Biomass

Roots

Coring

Distribution

Gazi

ABSTRACT

Estimation of total biomass in woody ecosystems is important because of its relevance to nutrient turnover and the potential to store carbon. Most work on mangrove biomass, particularly in the Western Indian Ocean Region, has concentrated on the above-ground component; comparatively little is known on below-ground biomass. The current study was conducted at Gazi bay on the southern coast of Kenya. The objective was to determine the below-ground biomass of three species of mangrove, *Rhizophora mucronata* Lamarck, *Avicennia marina* (Forsk.) Vierh and *Sonneratia alba* J. Smith, in natural and replanted stands. The effects of distance from the tree base and of soil depth on root biomass and size distributions were also studied using coring. Live below-ground biomass (mean \pm S.E.) ranged from 7.5 ± 0.4 t/ha to 35.8 ± 1.1 t/ha, 48.4 ± 0.7 t/ha to 75.5 ± 2.0 t/ha and 39.1 ± 0.7 t/ha to 43.7 ± 1.7 t/ha for *R. mucronata*, *S. alba* and *A. marina*, respectively, depending on the age of the stand. Including dead roots produced total biomass values of 34.9 ± 1.8 – 111.5 ± 5.6 t/ha, 78.9 ± 3.3 – 121.5 ± 7.3 t/ha and 49.4 ± 1.1 – 84.7 ± 5.4 t/ha for *R. mucronata*, *S. alba* and *A. marina*. These values imply carbon contents of live roots ranging between 3.8 ± 0.2 C t/ha and 17.9 ± 0.6 C t/ha, 24.2 ± 0.4 C t/ha and 37.7 ± 1.0 C t/ha and 19.5 ± 0.4 C t/ha and 21.9 ± 0.9 C t/ha for *R. mucronata*, *S. alba* and *A. marina* stands, respectively, and 17.4 ± 0.9 C t/ha and 55.7 ± 2.8 C t/ha, 39.4 ± 1.7 C t/ha and 60.7 ± 3.6 C t/ha and 24.7 ± 0.6 C t/ha and 42.4 ± 2.9 C t/ha for *R. mucronata*, *S. alba* and *A. marina* stands, respectively if dead roots are included. Stand densities were 4650 ± 177 stems/ha, 3800 ± 212 stems/ha and 3567 ± 398 stems/ha for *R. mucronata* 6-year old, 12-year-old and natural stands respectively. Mean stem diameter, and basal area were highest in the 12-year-old plantation while below-ground root biomass increased with age. Stand density for *S. alba*, was highest in the 12-year-old plantation (7900 ± 141 stems/ha) while the 9-year-old stand had trees with the largest diameter (7.7 ± 0.9 cm). Below-ground biomass was highest in the 12-year old (75.5 ± 2.0 t/ha) and lowest in the natural stand (48.4 ± 0.7 t/ha). Stand density for *A. marina* was highest in the 12-year-old plantation (4300 ± 919 stems/ha) while mean stem diameter (7.9 ± 0.7 cm) and basal area (16.2 ± 2.1 m²/ha) were highest in the natural stand. Below-ground biomass in the 12-year-old (43.7 ± 1.7 t/ha) and natural stands (39.1 ± 0.7 t/ha) was similar. Root densities decreased with soil depth and with distance from the base of trees for all species and stands. Fine roots (diameter <5 mm) constituted between 24% and 45% of the total stand live root biomass. The information generated is important in establishing the total biomass and thus the potential amount of carbon sequestered by mangroves in the study area.

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1. Introduction

Estimation of biomass in woody ecosystems, such as mangroves, is required for a number of reasons. Foresters are interested

in the yield of wood as a function of age, stand density and other factors. Ecologists require information about stand biomass for its relevance to nutrient turnover, stand structure and function and competition studies. Ecophysiologicalists have used biomass as an indicator of atmospheric and soil pollution input and forest health (Komiya et al., 2002). More recently, there has been much discussion on the potential for woody ecosystems to store carbon and contribute to mitigation strategies to offset carbon emissions (Yanai et al., 2006; Eamus et al., 2002, 2000; Vogt et al., 1998).

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Although mangroves occupy only 0.4% of the forested areas globally, they are important sinks for atmospheric CO₂ along tropical coastlines (Bouillon et al., 2008; Komiyama et al., 2002); they are among the most productive ecosystems on earth and account for about 11% of the total input of terrestrial C into the oceans (Jennerjahn and Ittekkot, 2002). Mangroves are estimated to store carbon in excess of 4.0 gigatons (Ong, 1993; Twilley et al., 1992), although this estimate is likely to be too low, given that ~112 Tg C a⁻¹, or >50% of all the carbon fixed by mangroves annually, remains unaccounted for (Bouillon et al., 2008). This carbon is stored in both above and below-ground tree components as well as in the sediment (Twilley et al., 1992). In contrast to terrestrial forests, root production may contribute half or more of the total standing biomass in mangroves (Briggs, 1977). Because mangroves grow in saturated, low oxygen soils, much of the carbon stored in roots resists decay and can form long-term sinks as mangrove peat (Middleton and McKee, 2001). Hence understanding the controls on below-ground biomass is essential in determining the carbon dynamics and carbon storage potential of mangrove ecosystems. While there is a substantial literature on the above-ground biomass of mangrove forests (see e.g. Soares and Novelli, 2005; Zianis and Mencuccini, 2003; Komiyama et al., 2002; Clough, 1992), fewer studies have considered below-ground biomass (but see Comley and McGuinness, 2005; Ong et al., 2004; Alongi and Dixon, 2000; Komiyama et al., 2000; Saintilan, 1997a,b), because of the logistical difficulties involved.

Coarse roots generally contribute more to total biomass than fine roots in terrestrial systems (Eamus et al., 2002). However, in mangroves fine roots may contribute up to 66% of the total root biomass (Komiyama et al., 1987). The fine roots of trees such as the mangroves are concentrated on lateral branches that arise from perennial roots. They are important in the acquisition of water and essential nutrients, and at the ecosystem level, they make a significant contribution to biogeochemical cycling. Estimates of root biomass must therefore differentiate between coarse and fine root biomass (Komiyama et al., 2000).

Though distribution of roots with soil depth is difficult to measure in terrestrial forests (Yanai et al., 2006), this is relatively easy in mangroves using coring methods, because mangrove roots

and substrate are soft and can be penetrated using a corer (Komiyama et al., 1987). The distribution of root biomass with distance from tree base is not well studied even in terrestrial forests (Yanai et al., 2006). The few relevant studies show that most coarse root biomass is found close to the stems (Millikin and Bledsoe, 1999). Fine roots, however, can extend long distances away from the stem and their spread may reflect the distribution of nutrients in the soil (Yanai et al., 2006) and are less sensitive to distance from tree base (Eamus et al., 2002; Millikin and Bledsoe, 1999).

The present study complements previous work at Gazi bay on above-ground biomass (Slim et al., 1997; Kirui et al., 2006) in arriving at estimates of the total biomass of mangrove species present in the bay. This is among the few studies (Kairo et al., 2008) in eastern Africa to investigate below-ground root biomass of mangroves. The main objectives were to determine the below-ground biomass of mangroves in both replanted and natural stands, exploring the effects of stand age and history (planted or natural) on root biomass. Differences between species, and the effects of soil depth and distance from the tree base on biomass and root size distribution were also examined.

2. Materials and methods

2.1. Site description

This study was conducted at Gazi bay (4°25' S and 39°30' E), on the southern coast of Kenya about 50 km from Mombasa city in Kwale District (Fig. 1). The bay is sheltered from waves by the presence of the Chale peninsula to the east and a fringing coral reef to the south (Bosire et al., 2004). The climate in Gazi bay is principally influenced by monsoon winds. Total annual precipitation varies between 1000 mm and 1600 mm with a bimodal pattern of distribution. The long rains fall from April to August under the influence of the southeast monsoon winds, while the short rains fall between October and November under the influence of the northeast monsoon winds. It is normally hot and humid with an average annual air temperature of about 28 °C with little seasonal variation. Air temperature in Gazi bay varies

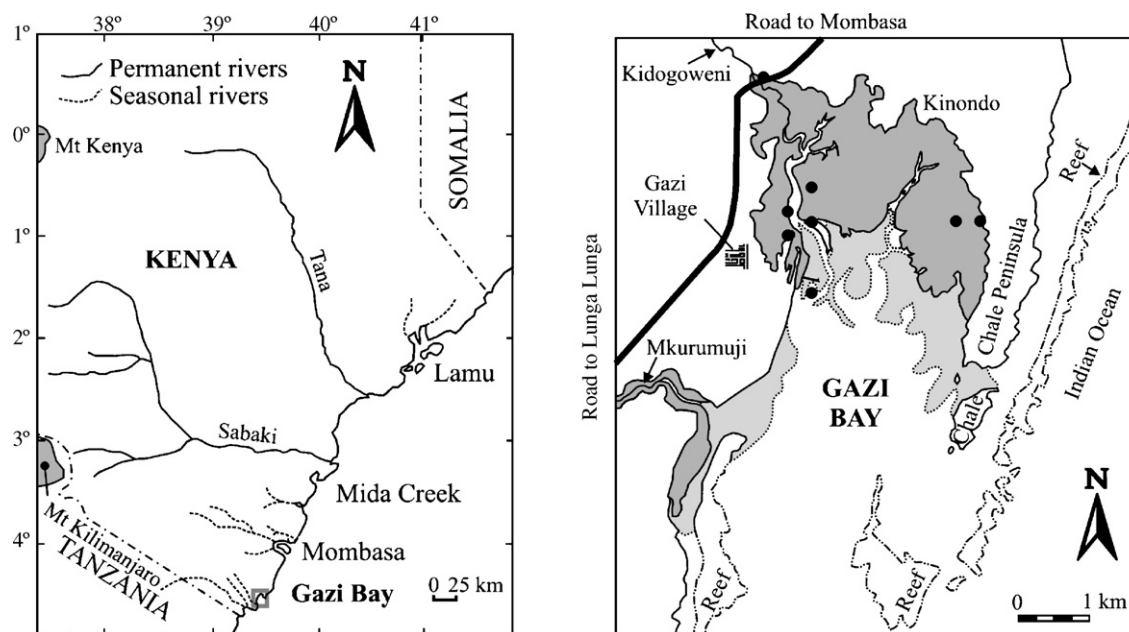


Fig. 1. Map of the Kenyan coast showing the study site (Gazi bay) and the locations of sampling. Key: (•) sampling location (Adapted from Bosire et al., 2004).

Table 1
Monospecific mangrove stands of different ages used in the present study

	6 years	9 years	12 years	Natural stand
<i>A. marina</i>			✓	✓
<i>R. mucronata</i>	✓		✓	✓
<i>S. alba</i>		✓	✓	✓

✓: Age and species sampled for the study.

between 24 °C and 39 °C. Relative humidity is about 95% due to the close proximity to the sea. The mangrove is not continuously under the direct influence of freshwater because the two rivers, Kidogoweni in the north and Mkurumji in the south draining into the bay are seasonal and dependent on the amount of rainfall inland. Groundwater seepage is also restricted to a few points.

All the nine species of mangroves described in Kenya occur in Gazi (Kairo, 1995). The dominant species are *Rhizophora mucronata* Lamarck and *Ceriops tagal* (Perr) C.B. Robinson (Kairo, 2001). The mangrove forests of Gazi bay were exploited for industrial extraction in the 1970s, which left large denuded areas with no natural regeneration (Kairo, 1995; Bosire et al., 2004). The mangroves at Gazi bay are still threatened by over-harvesting of wood products for firewood and building poles (Abuodha and Kairo, 2001). Recent surveys indicate that 70% of the mangroves of Gazi are degraded (Dahdouh-Guebas et al., 2004), with some of the affected areas requiring urgent reforestation. In order to enhance regeneration, trial mangrove plantations were initiated in degraded intertidal areas in 1991 (Kairo, 1995). Further monospecific stands of *R. mucronata*, *Bruguiera gymnorrhiza* (Lam) (Kairo, 1995), *Avicennia marina* (Forsk.) Vierh, *Sonneratia alba* J. Smith and *C. tagal* were planted in denuded mudflats between 1994 and 2000 (Bosire et al., 2004; Kairo, 1995). The present study investigated root biomass of *R. mucronata*, *S. alba* and *A. marina* in monospecific natural and reforested stands. Replanted stands of three different ages (6 and 12-year-old for *R. mucronata*, 9 and 12-year-old for *S. alba* and a 12-year-old stand for *A. marina*) were studied (Table 1).

2.2. Estimation of below-ground biomass

A modified version of Saintilan's (1997a,b) coring method was used. Two 10 m × 10 m plots were marked in each age category of reforested stands, and three in each natural stand (Table 1). A total of seven plots in *R. mucronata*, five in *A. marina* and seven in *S. alba* stands were sampled. Four trees were randomly selected for root coring within each plot. A ring was drawn around the base of each tree and was subsequently subdivided into three parts at 120°. For each tree, three cores (60 cm deep and 15.6 cm diameter) were taken from each of three horizontal positions; at the tree base, at mid canopy and at the edge of the canopy. Hence, a total of 36 cores were taken per plot. Cores were divided into three 20 cm vertical categories: 0–20 cm, 20–40 cm, and 40–60 cm. Each sample was washed over a 1 mm mesh and live and dead roots separated. Live roots were then sorted into diameter classes: <5 mm, 5–10 mm, 10–20 mm, 20–30 mm, 30–40 mm and >40 mm. All roots were weighed fresh. A representative fresh sub-sample from each root class was oven dried at 80 °C to a constant weight and re-weighed. Results obtained were pooled to obtain dry root biomass per unit ground area.

The calculations were based on the dry weights obtained. For root biomass at the base of tree stems, the basal area of the trees (G , per m²) within the 100 m² plot was determined using the conventional basal area formula (Cintron and Schaeffer, 1984);

$$G = \sum \frac{[(D/2)^2 \pi]}{10,000} \text{ (m}^2/100 \text{ m}^2) \quad (1)$$

where D (cm) was diameter at breast height (1.3 m above ground) of the trees in the plot.

Basal area was summed over all trees within each plot. The area occupied by a single core (A_{core}) was 0.0191 m² (15.6 cm diameter). Root biomass at the middle (M_{middle}) and edge (M_{edge}) of the tree canopy for all species were found not to differ significantly (see Section 3) and were therefore pooled together and considered as root biomass “between” the trees in the calculations, i.e.:

$$M_{\text{between}} = \frac{M_{\text{middle}} + M_{\text{edge}}}{2} \quad (2)$$

Therefore,

$$M_{\text{TOT}}^{\text{plot}} = M_{\text{base}} \frac{G}{A_{\text{core}}} + M_{\text{between}} \frac{(100 - G)}{A_{\text{core}}} \text{ (kg/m}^2) \quad (3)$$

where $M_{\text{TOT}}^{\text{plot}}$ and M_{base} were the total mass of roots for the 100 m² plot and the mass of roots at the base of trees, respectively. Values per hectare were then correspondingly obtained.

2.3. Forest structure

In each of the above plots, structural measurements included tree heights (m) and diameter, D (cm). Trees greater than 5 cm (D) within each plot were measured using a forest calliper. Stem diameter was measured 30 cm above the highest prop roots for *R. mucronata* and at 1.3 m above ground for the other two species. Tree heights were measured to the nearest meter, using a graduated pole. Tree basal area (BA) and mean D (cm) were derived from diameter measurements (Cintron and Schaeffer, 1984).

2.4. Data analyses

Statistical analyses were carried out with the MiniTab statistical package (Version 14). Separate comparisons between mean below-ground biomass found in different stand ages (for each species) and between species (with biomass pooled for all ages within each species) were done using one-way ANOVA. The effects of distance from the tree base, soil depth and diameter class (size of roots) were compared using General Linear Models for both live and dead roots, for each species separately. Below-ground root size classes were also compared over depth and stand ages of each species. All data were tested for normality and homogeneity of variances. *Post-hoc* means comparisons were evaluated by Bonferroni test statistic ($P < 0.05$). The below-ground root biomass per unit area for each species and stand age was calculated using the Excel statistical package.

3. Results

3.1. Effect of stand age, density, mean tree diameter (D) and basal area on below-ground biomass

3.1.1. *R. mucronata*

Stand density in the 6-year-old plantation was 4650 ± 177 (mean \pm S.E.; here and in all subsequent averages) stems/ha (largely made up of small stem diameter trees) and it was 3567 ± 398 and 3800 ± 212 stems/ha in the natural and 12-year-old stands, respectively. Mean diameter (cm) and basal area were highest in the 12-year-old plantation (Table 2). Below-ground root biomass differed between stands of different age, with values increasing with age. The natural stand yielded the greatest live below-ground biomass (35.8 ± 1.1 t/ha) and the 6-year-old stand the lowest (7.5 ± 0.4 t/ha).

Table 2Stand density, mean tree diameter (*D*, cm), basal area and total below-ground biomass for (a) *Rhizophora mucronata*, (b) *Sonneratia Alba* and (c) *Avicennia marina* stands

Stand age (years)	Stand density (stems/ha)	Mean <i>D</i> (cm)	Basal area (m ² /ha)	Dry root biomass (t/ha)	Sample size (<i>n</i>)
a) <i>R. mucronata</i>					
6	4650 ± 177 ^a	2.4 ± 0.3 ^a	2.3 ± 0.6 ^a	7.5 ± 0.4 ^a	47
12	3800 ± 212 ^a	7.9 ± 0.4 ^c	19.5 ± 0.6 ^b	24.9 ± 1.6 ^b	38
Natural	3567 ± 398 ^a	6.5 ± 0.2 ^b	17.0 ± 1.4 ^b	35.8 ± 1.1 ^c	36
b) <i>S. alba</i>					
9	2300 ± 174 ^a	7.7 ± 0.9 ^b	12.6 ± 1.4 ^a	53.4 ± 1.7 ^{ab}	33
12	7900 ± 141 ^b	5.4 ± 0.4 ^a	22.7 ± 3.2 ^b	75.5 ± 2.0 ^b	69
Natural	3067 ± 283 ^a	7.4 ± 0.5 ^b	15.9 ± 1.5 ^a	48.4 ± 0.7 ^a	35
c) <i>A. marina</i>					
12	4300 ± 919 ^b	5.6 ± 0.4 ^a	11.6 ± 0.7 ^a	43.7 ± 1.7 ^a	31
Natural	3133 ± 501 ^a	7.9 ± 0.7 ^b	16.2 ± 2.1 ^b	39.1 ± 0.7 ^a	43

Means within a column per species followed by different superscripts differ ($P < 0.05$) (mean ± S.E.).

3.1.2. *S. alba*

Stand density and basal area were highest in the 12-year-old plantation (7900 ± 141 stems/ha; 22.7 ± 3.2 m²/ha) while the 9-year-old plantation had the trees with the largest diameter (7.7 ± 0.9 cm) but the lowest stand density (2300 ± 174 stems/ha, Table 2). For this species, the natural stand showed the lowest mean below-ground root biomass, with the 9-year-old stand intermediate and the 12-year-old the highest.

3.1.3. *A. marina*

Though the 12-year-old plantation had the greatest stand density (4300 ± 919 stems/ha), it was composed of small trees with small stem diameters (5.6 ± 0.4 cm) compared to that of natural stands (7.9 ± 0.7 cm). Natural stands also had on average the highest basal area (16.2 ± 2.1 m²/ha) (Table 2). However, the 12-year-old stand yielded similar below-ground biomass (43.7 ± 1.7 t/ha) to that of the natural stand (39.1 ± 0.7 t/ha).

3.2. Comparison of yields of similar age stands

Mean below-ground biomass recorded for 12-year-old stands showed greater yield for *S. alba* (75.5 ± 2.0 t/ha) followed by *A. marina* (43.7 ± 1.7 t/ha) and the lowest was for *R. mucronata* (24.9 ± 1.6 t/ha). Root biomass yields in natural stands for the three species (*R. mucronata*, 35.8 ± 1.1 t/ha; *S. alba*, 48.4 ± 0.7 t/ha and *A. marina*, 39.1 ± 0.7 t/ha) did not differ significantly ($P > 0.05$; Table 2).

3.3. Distribution of live and dead root biomasses (t/ha) with distance from tree base and soil depth

Live root biomasses and root class diameters decreased with distance from tree base in the order Base > middle = edge in all stands (Table 3). Similarly, live root biomasses decreased rapidly with soil depth; 0–20 > 20–40 > 40–60 cm. The highest root biomass (44–67% of total live root biomass) was in the first 0–20 cm soil depth in all stands and lowest (4–20%) in the 40–60 cm soil depth (Table 4). These yields corresponded with reduction in root diameter class with soil depth; most of the coarse roots were restricted to the top soil layer.

Distribution of dead roots in the 6-year-old *R. mucronata* stand increased with soil depth. This stand was established after a torrential summer during an 'El Niño' that destroyed a pre-existing natural stand, suggesting a substantial contribution of biomass from the previous stand. Biomass of dead roots of other stands did not show any vertical or horizontal trends.

3.4. Live root biomass (t/ha) in relation to root size class diameter

Root biomasses decreased with increase in root diameter (Table 5). The <5 mm diameter class contributed 24%, 45% and 42% of total root biomass for *R. mucronata*, *S. alba* and *A. marina* stands respectively. Similarly, yields of roots <5–20 mm diameter contributed 86% of the total root biomass of all species. Roots

Table 3Live and dead root biomass (t/ha) distribution with distance from tree base in (a) *Rhizophora mucronata*, (b) *Sonneratia alba* and (c) *Avicennia marina* stands

Distance from tree base	6-year-old		12-year-old		Natural	
	Live roots (t/ha)	Necromass (t/ha)	Live roots (t/ha)	Necromass (t/ha)	Live roots (t/ha)	Necromass (t/ha)
(a) <i>R. mucronata</i>						
Tree base	3.4 ± 0.2 ^b	32.9 ± 2.4 ^a	10.4 ± 0.5 ^b	3.5 ± 0.1 ^a	13.9 ± 0.5 ^b	12.2 ± 0.8 ^b
Mid canopy	2.2 ± 0.1 ^a	33.7 ± 1.8 ^a	7.3 ± 0.5 ^a	3.2 ± 0.1 ^a	11.1 ± 0.3 ^a	10.6 ± 0.5 ^a
Edge canopy	1.9 ± 0.1 ^a	37.4 ± 1.2 ^a	7.1 ± 0.6 ^a	3.3 ± 0.1 ^a	10.7 ± 0.3 ^a	9.8 ± 0.7 ^a
	9-year-old		12-year-old		Natural	
(b) <i>S. alba</i>						
Tree base	21.9 ± 0.7 ^b	20.0 ± 1.6 ^a	27.1 ± 0.6 ^b	14.1 ± 0.9 ^a	18.1 ± 0.3 ^b	11.8 ± 0.9 ^a
Mid canopy	16.3 ± 0.5 ^a	27.6 ± 1.9 ^b	24.9 ± 0.8 ^a	16.0 ± 1.5	15.5 ± 0.2 ^a	9.4 ± 1.0 ^a
Edge canopy	16.2 ± 0.5 ^a	20.4 ± 3.3 ^a	23.5 ± 0.6 ^a	14.8 ± 0.9 ^a	14.9 ± 0.2 ^a	9.2 ± 1.1 ^a
			12-year-old		Natural	
(c) <i>A. marina</i>						
Tree base			17.5 ± 0.5 ^b	14.4 ± 1.2 ^a	15.5 ± 0.4 ^c	4.0 ± 0.2 ^a
Mid canopy			13.6 ± 0.5 ^a	12.6 ± 1.6 ^a	13.0 ± 0.2 ^b	3.6 ± 0.2 ^a
Edge canopy			12.7 ± 0.5 ^a	14.1 ± 1.3 ^a	10.7 ± 0.2 ^a	2.8 ± 0.1 ^a

Means within a column per species followed by different superscripts differ ($P < 0.05$) (mean ± S.E.).

Table 4Live and dead root biomass (t/ha) distribution with soil depth in (a) *Rhizophora mucronata*, (b) *Sonneratia alba* and (c) *Avicennia marina* stands

Soil depth (cm)	6-year-old		12-year-old		Natural	
	Live roots (t/ha)	Necromass (t/ha)	Live roots (t/ha)	Necromass (t/ha)	Live roots (t/ha)	Necromass (t/ha)
(a) <i>R. mucronata</i>						
0–20	3.8 ± 0.3 ^c	14.3 ± 1.0 ^a	10.9 ± 0.8 ^c	3.4 ± 0.3 ^a	17.7 ± 0.6 ^c	10.4 ± 0.7 ^a
20–40	2.5 ± 0.2 ^b	23.6 ± 1.0 ^b	8.8 ± 0.5 ^b	3.0 ± 0.2 ^a	11.7 ± 0.4 ^b	10.9 ± 0.6 ^a
40–60	1.2 ± 0.1 ^a	66.1 ± 4.2 ^c	5.2 ± 0.5 ^a	3.6 ± 0.3 ^a	6.4 ± 0.3 ^a	11.3 ± 0.7 ^a
	9-year-old		12-year-old		Natural	
(b) <i>S. alba</i>						
0–20	35.6 ± 1.4 ^c	20.3 ± 4.3 ^a	50.6 ± 0.9 ^c	12.2 ± 1.0 ^a	31.4 ± 0.7 ^c	10.8 ± 1.0 ^a
20–40	13.0 ± 0.6 ^b	24.7 ± 2.8 ^a	21.8 ± 1.0 ^b	18.9 ± 2.0 ^b	12.4 ± 0.3 ^b	10.1 ± 1.2 ^a
40–60	4.9 ± 0.2 ^a	23.0 ± 1.3 ^a	3.0 ± 0.1 ^a	13.8 ± 1.0 ^a	4.6 ± 0.3 ^a	10.0 ± 1.0 ^a
			12-year-old		Natural	
(c) <i>A. marina</i>						
0–20			28.5 ± 1.2 ^c	9.7 ± 0.4 ^a	20.6 ± 0.6 ^c	4.4 ± 0.2 ^a
20–40			12.6 ± 0.8 ^b	21.6 ± 2.6 ^b	14.5 ± 0.4 ^b	3.3 ± 0.2 ^a
40–60			2.6 ± 0.3 ^a	9.7 ± 1.3 ^a	4.0 ± 0.2 ^a	2.6 ± 0.2 ^a

Means within a column per species followed by different superscripts differ ($P < 0.05$) (mean ± S.E.).**Table 5**Contribution of live root diameter classes to root biomass (t/ha) in (a) *Rhizophora mucronata*, (b) *Sonneratia Alba* and (c) *Avicennia marina* stands

Stand age (years)	Diameter class (mm)					
	<5	5–10	10–20	20–30	30–40	>40
(a) <i>R. mucronata</i> (t/ha)						
6	3.0 ± 0.2 ^a	1.2 ± 0.1 ^a	2.3 ± 0.2 ^c	0.7 ± 0.1 ^a	0.3 ± 0.1 ^a	0.0 ± 0.0 ^a
12	6.1 ± 0.3 ^b	2.8 ± 0.1 ^b	7.6 ± 0.4 ^b	6.6 ± 0.6 ^b	1.8 ± 0.4 ^b	0.0 ± 0.0 ^a
Natural	7.2 ± 0.2 ^b	5.5 ± 0.2 ^c	12.8 ± 0.5 ^a	8.3 ± 0.4 ^b	1.4 ± 0.1 ^b	0.7 ± 0.2 ^b
(b) <i>S. alba</i> (t/ha)						
9	28.2 ± 1.0 ^b	9.3 ± 0.4 ^a	15.0 ± 1.0 ^a	1.0 ± 0.3 ^a	0.0 ± 0.0 ^a	0.0 ± 0.0 ^a
12	28.6 ± 0.5 ^b	13.5 ± 0.4 ^a	18.1 ± 1.1 ^b	5.3 ± 0.4 ^c	0.1 ± 0.0 ^a	0.0 ± 0.0 ^a
Natural	15.1 ± 0.4 ^a	12.8 ± 0.4 ^a	15.5 ± 0.5 ^a	3.9 ± 0.1 ^b	0.6 ± 0.1 ^b	0.6 ± 0.2 ^b
(c) <i>A. marina</i> (t/ha)						
12	20.2 ± 1.4 ^a	16.3 ± 0.6 ^a	5.8 ± 0.2 ^a	1.3 ± 0.2 ^a	0.0 ± 0.0 ^a	0.0 ± 0.0 ^a
Natural	14.4 ± 0.8 ^a	13.8 ± 0.3 ^a	9.2 ± 0.3 ^b	1.4 ± 0.1 ^a	0.1 ± 0.0 ^a	0.0 ± 0.0 ^a

Means within a column per species followed by different superscripts differ ($P < 0.05$) (mean ± S.E.).

>40 mm in diameter were not recorded in planted stands. Generally, yields of younger planted stands were lower than that of old stands whereas biomass yields of the natural stands were similar to that of 12-year-old planted stands. It is not clear why biomass from 20–30 mm root class diameter was substantially high in *R. mucronata* and *S. alba* stands.

4. Discussion

4.1. Effect of stand age, density, diameter at breast height (D) and basal area on below-ground biomass

4.1.1. *Rhizophora mucronata*

Though mean D (cm) in the natural stand of *R. mucronata* was smaller than in the 12-year-old plantation, live below-ground biomass was higher (Table 2). This was probably because there were few trees with large D (cm) but many with small diameter trees leading to a reduced mean D (cm). The 12-year-old plantation had even aged trees of similar D (cm) and therefore a higher mean D (cm) compared to the natural stand. However, the big trees in the natural stand probably contributed to a comparatively higher biomass. The natural stand also showed the highest live below-ground biomass because of the presence of more roots in coarse root classes (>10 mm) compared to that in 6- and 12-year-old plantations.

Below-ground root biomass (7.5 ± 0.4 – 35.8 ± 1.1 t/ha) in *R. mucronata* stands were low compared to the range reported for mangroves around the world (Table 6). However, comparisons with other studies are problematic because of methodological differences in estimating below-ground biomass. In Thailand, a 25-year-old *R. apiculata* plantation yielded 35.6 t/ha below-ground root biomass (Alongi and Dixon, 2000) which is similar to the yield of the natural stand in the present study (35.8 ± 1.1 t/ha). However, a 5-year-old plantation in Thailand yielded 23.1 t/ha (Alongi and Dixon, 2000), which was much higher than the 7.5 ± 0.4 t/ha for the 6-year-old plantation in the present study.

In Cuban mangroves, total below-ground root biomass averaged 32.3 t/ha for *R. mucronata* forest (to a soil depth of 40 cm) (Alongi and Dixon, 2000), which is slightly lower than that of the natural stand in the present study (35.8 ± 1.1 t/ha). This may be attributed to the difference in sampling depth. The 40–60 cm soil depth samples accounted for 14.3–20% of the total root biomass in the present study depending on stand. Total below-ground biomass in Sawi Bay in Thailand ranged from 140.6 t/ha to 352.7 t/ha in a mature *R. mucronata* forest, and 140.6–269.9 t/ha for younger stands (Alongi and Dixon, 2000). However, 84–97% of the biomass was dead, hence the maximum live biomass was only ~56 t/ha. The conflation of dead and living biomass in a number of earlier studies (e.g. Briggs, 1977; Komiyama et al., 1987; Alongi and Dixon, 2000) may have led to

Table 6
Comparison of belowground biomass measured in mangrove forests around the world

Location	Sampling method	Species	Belowground biomass (t/ha)	Source
Australia	Soil cores	<i>A. marina</i>	147–160	Briggs (1977) ^a
Thailand	Trench	<i>R. apiculata</i>	338	Tabuchi et al. (1983)
Thailand	Trench and root density model	<i>R. mucronata</i> <i>S. alba</i>	243 32–172	Komiyama et al. (1987) ^b
Australia	Soil cores	<i>A. marina</i>	109–126	Mackey (1993) ^a
Australia	Stratified coring	<i>A. marina</i> <i>A. corniculatum</i>	70–166 35–106	Saintilan (1997a)
Australia	Soil cores	<i>A. marina</i> <i>A. corniculatum</i>	15–60 25–80	Saintilan (1997b)
Australia	Soil cores	<i>R. stylosa</i>	35–56	Alongi et al. (2000)
Dominican Republic	Soil cores	<i>R. mangle</i>	67.8	Sherman et al. (2003) ^b
Kenya	Soil cores	<i>R. mucronata</i> <i>A. marina</i> <i>S. alba</i>	8–25 ^c 43 ^d 53–76 ^e	Present study

^a Includes biomass of pneumatophores.

^b Data include live and dead root.

^c Age 6–12 years.

^d Age 12 years.

^e Age 9–12 years.

overestimation of the yields, especially given the refractory nature of mangrove root material (Middleton and McKee, 2001).

4.1.2. *Sonneratia alba*

The 12-year-old plantation of *S. alba* had the highest live below-ground biomass (75.5 ± 2.0 t/ha, Table 2). This was probably caused by the high density in this stand (7900 ± 141 stems/ha). High stand densities also resulted in a high basal area (22.7 ± 3.2 m²/ha) and correspondingly more root density per unit area compared to the natural stand. The 12-year-old plantation also yielded the highest below-ground biomass because of greater root biomass in larger size classes (10–20 mm) compared to the 9-year-old plantation and the natural stand. Yields from this study fall within the range 32.4–171.8 t/ha reported Komiyama et al. (1987, 2000), again including necromass (Table 6).

4.1.3. *Avicennia marina*

The 12-year-old plantation had slightly higher live below-ground biomass than the natural stand (Table 2). This may have been due to the high stand density (4300 ± 919 stems/ha) in the stand compared to that in the natural stand (3133 ± 501 stems/ha). Briggs (1977) and Mackey (1993) reported much higher biomasses (Table 6) although they included the biomass of pneumatophores. Studies excluding dead roots and pneumatophores, such as Alongi et al. (2000) have produced estimates comparable with those from the current study.

Overall, yields for the same age stand followed the following pattern; *S. alba* > *A. marina* > *R. mucronata*. This is probably because at the site *S. alba* is the seaward most species, hence is subjected to intensive wave action. Therefore, a higher root biomass could be beneficial for anchorage purposes and for support in the unstable substrate. Moreover, *S. alba* is the fastest growing and productive species at the site (Kairo, 2001). *R. mucronata* has previously been reported as having a relatively small proportion of live below-ground biomass (Clough, 1992). This is because, unlike most other mangrove species, *Rhizophora* species are supported by prop root system above the ground. Comparatively, *S. alba* and *A. marina* yielded more below-ground root biomass because of their extensive underground cable root systems whereas those of *R. mucronata* are spongy and soft.

4.2. Live root and necromass distribution with soil depth and distance from tree base

The vertical distribution patterns of live below-ground biomass in all three species were in line with those described for other mangrove forests (Komiyama et al., 2000). There was a high live root biomass in the 0–20 cm layer gradually decreasing with soil depth in all species (Table 4). In the present study, between 44% and 67% of the total root biomass was found in the upper 0–20 cm, with about 24–39% in the next 20–40 cm and 4–20% in the 40–60 cm. Concentration of root biomass in the upper 50 cm of sediment has also been reported before in mangroves (Clough, 1992; Komiyama et al., 2000). High live root biomass in the top sediment layer might be a physiological adaptation in mangroves to facilitate efficient uptake of water and nutrients from the soil surface layers, which are characterized by accumulation of organic matter and relatively large amounts of available nutrients as in terrestrial forests (Claus and George, 2005).

The contribution of fine roots to total biomass in all species was high. Generally, fine roots contributed between 24% and 45% of the total live below-ground root biomass, depending on species. This is in broad agreement with previous studies (46.4%, Komiyama et al., 1987 and 70%, Tabuchi et al., 1983). This suggests that fine roots are a primary contributor to total live root biomass in mangroves. In contrast, the proportion of fine roots biomass of total biomass in terrestrial forests is low ranging from 0.2% to 17.9% (Komiyama et al., 1987, 2000). The much higher standing biomass of fine roots in mangroves may be the result of higher fine root productivity, lower fine root mortality rate or a combination of both. In turn, higher productivity may be the result of higher overall mangrove productivity or of higher below-ground carbon allocation. Little process-based information is available that elaborates on the production process. However, the high amount of standing biomass in fine roots of mangroves is also accompanied by high amount of organic matter accumulation in the sediment (Alongi et al., 2000). This suggests that increased root productivity (probably coupled with reduced decomposition in the anoxic sediment environment) must be an important component in carbon sequestration of mangroves. Carbon

concentration in tissue is assumed to be 50% of the dry weight (Losi et al., 2003). Hence the carbon contained in live roots in the present study ranged between 3.8 ± 0.2 C t/ha and 17.9 ± 0.6 C t/ha, 24.2 ± 0.4 C t/ha and 37.7 ± 1.0 C t/ha and 19.5 ± 0.4 C t/ha and 21.9 ± 0.9 C t/ha for *R. mucronata*, *S. alba* and *A. marina* stands respectively. This would equate to 17.4 ± 0.9 – 55.7 ± 2.8 C t/ha, 39.4 ± 1.7 – 60.7 ± 3.6 C t/ha and 24.7 ± 0.6 – 42.4 ± 2.9 C t/ha for *R. mucronata*, *S. alba* and *A. marina* stands respectively when dead roots are included.

Most of the roots that are accumulated in mangrove soils are dead (Alongi et al., 2000, 2003). This is consistent with the proportion of dead roots 20–90% of the total biomass in the present study. However, the distribution of dead roots in the present study had a different pattern from that of live roots. The densities of dead roots in the natural and the 12-year-old *R. mucronata* stands did not differ with soil depth whereas the quantity of dead roots in the 6-year-old *R. mucronata* stand increased with depth (Table 4). The quantity of dead roots in the 6-year-old plantations averaged 104 ± 5.4 t/ha, compared to 32.5 ± 2.0 t/ha for the natural stands and 10 ± 0.3 t/ha for the 12-year-old plantations (Table 4). The 6-year-old *R. mucronata* plantation was on a site that suffered heavy mortalities during the El Niño event in 2000. The high amounts of dead roots may thus have accumulated from the previous degraded old stand. Dead root biomass in *A. marina* stands decreased with soil depth, in a similar pattern observed in live roots. This might reflect the faster decomposition rates of *A. marina* roots compared with those of other species at Gazi (M. Huxham, unpublished data). The vertical distribution of the dead roots in the other species supports the idea that they are refractory and able to provide long-term sequestration of carbon.

5. Conclusion

The total below-ground root biomass varied within species, depending on stand age, and among the species. Replanted stands of *S. alba* and *A. marina* recorded more below-ground biomass compared to natural stands. This difference could be attributed to the relatively degraded status of natural forests in Gazi bay. This highlights the potential role that can be played by reforestation and restoration in carbon sequestration by mangroves, since replanted mangroves are evidently capable of amassing stocks of soil carbon similar to those found in nearby natural forests within 12 years. The differences in below-ground biomass could also be attributed to the structural composition in *S. alba* stands. These stands had a higher plant density per unit area compared to *A. marina* and *R. mucronata* stands; unfortunately, the effects of age could not be entirely separated from other factors such as stand density in the current work. Consistent with previous work on mangroves in other regions, the present study showed the important contribution of fine roots to mangrove forests biomass, and that most of the roots are concentrated in the upper 20 cm of the sediment. It also shows that mangroves could have significant potential as carbon sinks through the rapid production of relatively refractory root material.

Acknowledgements

This study was facilitated through an AVIVA/Earthwatch Institute award to Dr. Huxham (Napier University, Edinburgh, UK), and was also supported by funds from The Leverhulme Trust and Earthwatch Institute. We are grateful to KMFRI for granting us permission to work in their Gazi Sub-centre and for providing field facilities.

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