ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Species mixing boosts root yield in mangrove trees

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Abstract Enhanced species richness can stimulate the productivity of plant communities; however, its effect on the belowground production of forests has scarcely been tested, despite the role of tree roots in carbon storage and ecosystem processes. Therefore, we tested for the effects of tree species richness on mangrove root biomass: thirty-two 6 m by 6 m plots were planted with zero (control), one, two or three species treatments of six-month-old *Avicennia marina* (A), *Bruguiera gymnorrhiza* (B) and *Ceriops tagal* (C). A monoculture of each species and the four possible combinations of the three species were used, with four replicate plots per treatment. Above- and belowground biomass was measured after three and four years' growth. In both years, the all-species mix (ABC) had significant overyielding of roots, suggesting complementarity mediated by differences in rhizosphere use amongst species. In year four, there was higher belowground than aboveground biomass in all but one treatment. Belowground biomass was strongly influenced by the presence of the most vigorously growing species, *A. marina*. These results demonstrate the potential for complementarity between fast- and slow-growing species to enhance belowground growth in mangrove forests, with implications for forest productivity and the potential for belowground carbon sequestration.

Keywords Root biomass · Overyielding · Mangrove forests · Species richness · Ecosystem function

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Introduction

The relationship between species richness and ecosystem functioning has generated much interest and debate, mainly due to concerns over the threat posed by human activities to biodiversity (Cardinale et al. 2004; Loreau et al. 2001; Schmid et al. 2008). The enhancement of ecosystem productivity by plant species richness has been attributed to mechanisms such as facilitation, niche complementarity and selection effects (Loreau 1998; Tilman et al. 2002). The increased productivity of a mixed-species assemblage compared to monocultures of the component species is referred to as overyielding, which can occur either as transitive (transgressive) or nontransitive. The former refers to a situation in which a mixture outproduces the highest yielding monoculture of the component species, while the latter occurs when the productivity of the mixture is higher than the weighted average productivity of the component species in the monoculture stands (Schmid et al. 2008; Pretzsch and Schütze 2009).

Most biodiversity-ecosystem function studies have been based on short-lived plants such as grasses (Tilman et al. 2001; Hector et al. 2002), probably because measurable trends could be established within a short period of time. For long-lived plants such as trees, species richness has the potential to enhance carbon sequestration by boosting biomass accumulation in woody tissues (Erskine et al. 2006; Vila et al. 2007; Pretzsch and Schütze 2009; Paquette and Messier 2011). Of the few studies that have focused on the functional role of tree species richness, most have considered effects of species richness on aboveground productivity (Erskine et al. 2006; Vila et al. 2007; Cavard et al. 2010; Ruiz-Jaen and Potvin 2010). Work on species richness and belowground productivity is very rare (Wang et al. 2002; Meinen et al. 2009a, b; Brassard et al. 2011).

Mangrove forests occur on tropical and subtropical coastlines, where they provide a wide range of goods and services (Ewel et al. 1998) and are important interfaces in the exchange of sediment, organic materials and gases between land, atmosphere and ocean (Alongi et al. 2004). Mangroves are among the most productive ecosystems on Earth (e.g. Twilley et al. 1992; Bouillon et al. 2008), with important roles in the global carbon cycle. They account for 11 % of the total input of terrestrial carbon into the oceans (Jennerjahn and Ittekkot 2002; Dittmar et al. 2006), despite comprising <1 % of the global forest coverage (Valiela et al. 2001; Spalding et al. 2010; Giri et al. 2011). Processes affecting mangrove productivity therefore have implications for global carbon sequestration (Twilley et al. 1992; Chmura et al. 2003; McLeod et al. 2011).

Differences in root structures between species are generally much more obvious in mangroves compared with terrestrial trees (Tomlinson 1986). For example, old-stand *Avicennia* forest has extensive, shallow root systems spanning several metres from the tree base and with emergent "pencil pneumatophores", while genera such as *Ceriops* and *Bruguiera* have clumped root systems with "knee roots" on the surface (Tomlinson 1986). Therefore, elevated diversity among mangrove trees has the potential to induce complementary effects and enhanced resource use efficiency, for instance by exploiting different soil zones, as has been demonstrated for some terrestrial forests (Jose et al. 2006; Brassard et al. 2011). Such effects should manifest themselves as enhanced belowground processes and biomass accumulation in mixed stands, and potentially also as enhanced root:shoot ratios (given the apparently greater differences in belowground as compared to aboveground architecture in mangroves). In terrestrial forests, belowground biomass usually accounts for ~ 20 % of the total biomass (e.g. Cairns et al. 1997; Yuan and Chen 2010). In contrast, the belowground biomass in mangroves often represents 30–60 % of the total biomass (Golley et al. 1962; Briggs 1977; Tamooh et al. 2008), and may even exceed aboveground biomass by a factor of four or more (Saintilan 1997a). Knowledge of belowground processes is therefore key to understanding mangrove ecosystem function. Mangrove roots are resistant to decay (Middleton and McKee 2001; Huxham et al. 2010) because of the anoxic conditions in which they grow (Alongi et al. 2004, 2005) and their high lignin content (Gleason and Ewel 2002). The high proportion of carbon allocated to belowground growth thus encourages the formation of stable deposits of mangrove peat (Cahoon et al. 2003; McKee et al. 2007), providing long-term carbon stores (Fujimoto et al. 1999) and a reservoir for nutrients in these oligotrophic forests (Alongi 2009).

Sampling belowground biomass in mangroves is logistically difficult (Komiyama et al. 1987, 2000; Saintilan 1997a; Tamooh et al. 2008), so belowground processes have scarcely been studied (McKee and Faulkner 2000; Gleason and Ewel 2002; Cahoon et al. 2003). Experimental work on the effects of species richness on ecosystem functions in mangroves is limited to a single paper on survival (Kirui et al. 2008).

We used experimental plantations to assess how tree species identity and species richness influences belowground biomass (henceforth abbreviated as BGB) and the root:shoot ratio (RSR) in young mangroves. We hypothesized that (1) BGB and (2) RSR will be enhanced in mixed-compared with single-species stands.

Materials and methods

Study site

The study was carried out at Gazi Bay, approximately 55 km south of Mombasa, Kenya. Gazi is a creek-type forest with 615 ha of mangroves dominated by *Rhizophora mucronata* (Lam), *Ceriops tagal* (Perr.) C. B. Robinson and *Avicennia marina* (Forsk.) Vierh. Freshwater input is intermittent: two seasonal rivers (Kidogoweni in the north and Mkurumuji in the south) discharge into the bay, and ground seepage is restricted to a few points (Tack and Polk 1999). A tidal creek, Kinondo, penetrates the forest on the eastern side. Gazi Bay has a semidiurnal tidal regime and mean spring tidal amplitude of 4.0 m. Gazi mangroves have been exploited for many years for wood fuel and building poles, leaving some areas denuded (Bosire et al. 2003; Dahdouh-Guebas et al. 2004; Kirui et al. 2008). Experimental planting in degraded mangroves of Gazi has been conducted with mixed success (Kairo et al. 2001, 2008). In this study, a 5 ha high-shore area at Kinondo was used for experimentation. This site was clear-felled ~ 35 years previously and had shown very limited natural regeneration since felling.

Experimental design

In August 2004, thirty-two 6 m by 6 m plots were established in two blocks with 16 plots in each block. The blocks were ~50 m apart and separated by a narrow ridge of higher ground vegetated by terrestrial grasses and shrubs. Within the blocks, experimental plots were set >6 m apart to minimize the chances of nonindependence (Kirui et al. 2008). Plots were randomly allocated to eight treatments, consisting of three monocultures, four different combinations of three mangrove species, *A. marina*, *Bruguiera gymnorrhiza* (Lamk.) and *C. tagal*—"A" (*Avicennia*), "B" (*Bruguiera*), "C" (*Ceriops*), "AB" (*Avicennia* and *Bruguiera*), "AC" (*Avicennia* and *Ceriops*), "BC" (*Bruguiera* and *Ceriops*) and "ABC" (all species)—and an unplanted control. The unplanted control plot is not dealt with in this study, as the control did not inform on root biomass. This replicated randomized block design had four replicates per treatment: two per block. Seedlings were grown in a nursery for at least six months and transplanted at 0.6 m apart, giving a total of 121 seedlings per plot. Nine mangrove species grow in Kenya. The three species used in the experiment are common on high shores and were selected since they all grow in mixed stands adjacent to the site.

Aboveground biomass (AGB)

In 2007 and 2008 (after three and four years' growth, respectively), 18 plants per plot were randomly selected for measurement. Sampling was carried out in the month of August in each consecutive year. For two- and three-species plots, nine and six plants per species were measured, respectively. Tree height, from the ground to the highest apical bud, and stem diameter were recorded. Stem diameter (D, mm) was measured at 30 cm aboveground for *Avicennia* and between the first and second internodes for *Bruguiera* and *Ceriops*. Height and diameter measurements were translated into dry-weight equivalents using allometric equations derived from young trees of each species harvested from contiguous natural forest outside the plots as follows:

Avicennia: biomass (g. dw) $= 0.6896 \times D^{2.0095}$ ($R^2 = 0.93$, $P < 0.001$, $df = 24$),
Bruguiera: biomass (g. dw) $= 0.6494 \times D^{1.7132}$ ($R^2 = 0.64$, $P = 0.002$, $df = 17$),
Ceriops: biomass (g. dw) $= 0.4112 \times D^{2.1032}$ ($R^2 = 0.94$, $P < 0.001$, $df = 7$).

Belowground biomass (BGB)

Belowground biomass was sampled in 2007 and 2008. Each plot was divided into four quarters and two randomly located cores (53 mm diameter, 40 cm deep) were taken from each quarter, giving eight subsamples per plot, which were pooled for analysis. Cores taken in 2007 from single-species plots were subdivided into 10 cm vertical sections to allow analysis of rooting depth traits for each species. Roots were extracted, gently rinsed, and separated into fine (≤ 3 mm diameter) and coarse (>3 mm diameter) portions; their fresh and dry weights (80 °C for 24 h) were determined. Dead roots were very scanty and hence were not included in the analysis. All roots found were attributed to experimental plants, as there were no mangrove trees (or other vascular plants) when plots were established (Kirui et al. 2008). Initial attempts to identify individual root fragments to species in mixed-species treatments proved unreliable, so roots in mixed plots could not be credited to individual species. The aboveground roots were not sampled since they were sparsely present.

Data analyses

The effects of species mix, treatment and age (year) on total root biomass, total aboveground biomass and RSR were analysed using repeated-measures ANOVA with treatment as fixed and block and age as random factors. Values for AGB, BGB and RSRs were square-root transformed to conform to the assumptions of normality and homogeneity of variances. Multiple comparisons (Tukey tests) were then performed for the significant terms, and separate ANOVA tests were also performed on data from the two years.

Overyielding was assessed by calculating the ratio of the observed (P_{or}) to the expected (P_{er}) root biomass for each two- and three-species plot. P_{er} was calculated as the proportion-weighted average of the root biomass of each component species in its pure stand (Pretzsch and Schütze 2009): $P_{er} = \sum(P_{ori}/m_i)$, where $P_{er} =$ expected root biomass in the mixture, $P_{ori} =$ observed root biomass of species i in monoculture and $m_i =$ the proportion of species i in the mixed stand at sampling. The ratio $P_{or}{:}P_{er}$ gives a measure of overyielding such that $P_{or}{:}P_{er} > 1$, <1 or $=1$ represent cases of overyield, underyield and proportional yield, respectively. Transitive (transgressive) overyielding (R) was assessed by the ratio of the observed root biomass of the mixture (P_{mix}) to the observed root biomass of the highest yielding monocultures of the component species (P_{mono}); i.e. $R = P_{mix}{:}P_{mono}$. The responses of BGB were tested for significant species richness effects by testing for significant deviation from $P_{or}{:}P_{er} = 1.0$. Vertical biomass distribution profiles for the monoculture plots were compared using chi-squared tests for heterogeneity. All data analyses were performed with SAS 12 or Minitab 14 software.

Results

Aboveground biomass

Average aboveground biomass ranged from 64.4 to 466.6 g m^{-2} and from 84.0 to 672.6 g m^{-2} in years three and four, respectively (Fig. 1). There were significant differences between the treatments and years ($F_{6,14} = 9.5$, $P = 0.008$; $F_{1,14} = 120$, $P = 0.019$; respectively) with no significant interaction. After four years of growth, A and AC treatments had significantly higher AGB than B and BC, while ABC differed significantly from the B treatment only (multiple comparisons; $P < 0.05$, Fig. 1).

Belowground biomass

Belowground biomass ranged from 15 to 436 and from 128 to 847 g m^{-2} after three and four years, respectively. There were significant differences in BGB between treatments and years ($F_{6,14} = 435$, $P < 0.001$; $F_{1,14} = 88$, $P < 0.001$) with no significant interactions. Post hoc analyses after three years showed that the A and ABC

Fig. 1 Mean (±1 95 % CI) above- (AGB) and belowground (BGB) biomass and RSR for plots with species richness treatments of three mangrove trees: *Avicennia* (A), *Bruguiera* (B) and *Ceriops* (C); n = 4 plots/treatment. *Different letters above bars* indicate a significant difference between these treatments at α = 0.05. †RSR of treatment B was significantly higher than those of all other treatments after four years

treatments had significantly higher total BGB than B, C and BC, while the BGB of AC only differed significantly from BC (multiple comparisons; $P < 0.05$, Fig. 1). After four years, the A and AB treatments registered significantly higher biomass than BC, whilst the BGB of the AC and ABC treatments was significantly higher than that of the C and BC treatments (multiple comparisons; $P < 0.05$, Fig. 1). Course roots constituted the bulk of the biomass in all treatments and both years, with fine roots ranging from 5 to 35 % of total weight (Table 1).

Root:shoot ratio (RSR)

The RSR ranged from 0.2 to 1.1 (mean 0.7 ± 0.2) and from 0.8 to 4.5 (mean 1.7 ± 0.7) after three and four years, respectively. There was a significant effect of year ($F_{1,14} = 25$, $P < 0.001$) and a significant treatment × year interaction ($F_{6,14} = 3.6$, $P = 0.023$), reflecting a large increase in RSR in treatment B after four years (Fig. 1).

Root yield

Fine and coarse roots and total root biomass for the ABC treatment showed significant overyielding in both years (one-way *t* tests; $P < 0.05$; Fig. 2). The AC treatment showed significant overyielding for coarse roots and total root biomass in year four (one-way *t* tests; $P < 0.05$; Fig. 2). The BC treatment had a significant underyield of coarse roots after three years ($t = -6.4$, $P = 0.008$; Fig. 2). No mixed-species treatment had significant transgressive overyielding relative to the corresponding highest yielding monocultures of the component species (Fig. 3).
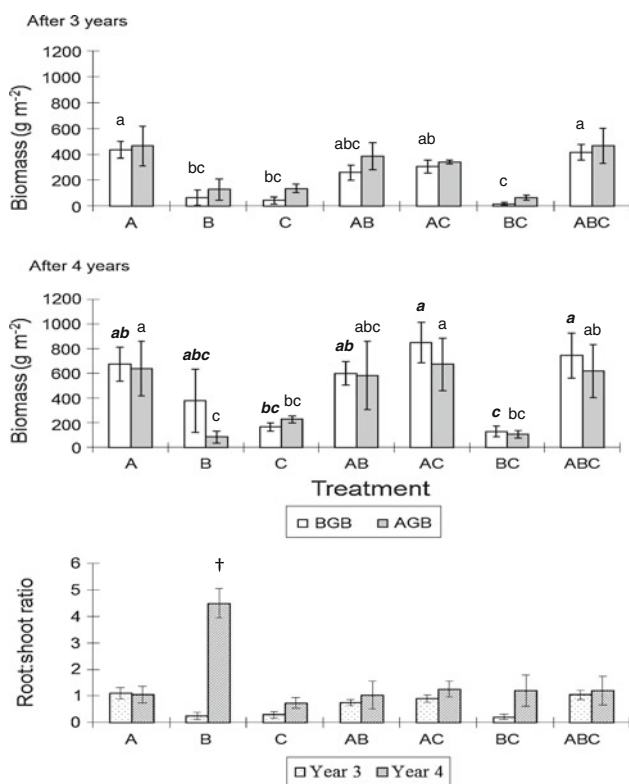
Table 1 Mean (±1 SE) percentage contributions of fine and coarse roots to the total belowground biomass of the mangrove biodiversity plantations at Gazi, Kenya

Treatment	Year three		Year four	
	Fine roots (≤3 mm)	Coarse roots (>3 mm)	Fine roots (≤3 mm)	Coarse roots (>3 mm)
Avicennia	17 ± 2	83 ± 2	23 ± 7	77 ± 7
Bruguiera	34 ± 22	66 ± 22	5 ± 2	95 ± 2
Ceriops	20 ± 13	80 ± 13	19 ± 5	81 ± 5
Avicennia–Bruguiera	20 ± 5	80 ± 5	21 ± 4	79 ± 4
Avicennia–Ceriops	17 ± 3	83 ± 3	18 ± 4	82 ± 4
Bruguiera–Ceriops	76 ± 24	24 ± 24	35 ± 22	65 ± 22
Avicennia–Bruguiera–Ceriops	15 ± 3	85 ± 3	23 ± 3	77 ± 3

Fig. 2 Belowground root overyielding of mixed mangrove tree species stands after three and four years' growth: values >1 indicate overyielding. *Crossbars* show the mean values, *boxes* represent 25 and 75 % percentiles and *vertical lines* represent extremities. *Avicennia–Bruguiera* (AB), *Avicennia–Ceriops* (AC), *Bruguiera–Ceriops* (BC) and *Avicennia–Bruguiera–Ceriops* (ABC); $n = 4$ plots/treatment. Symbols (** and *) indicate significance at $\alpha = 0.01$ and $\alpha = 0.05$, respectively
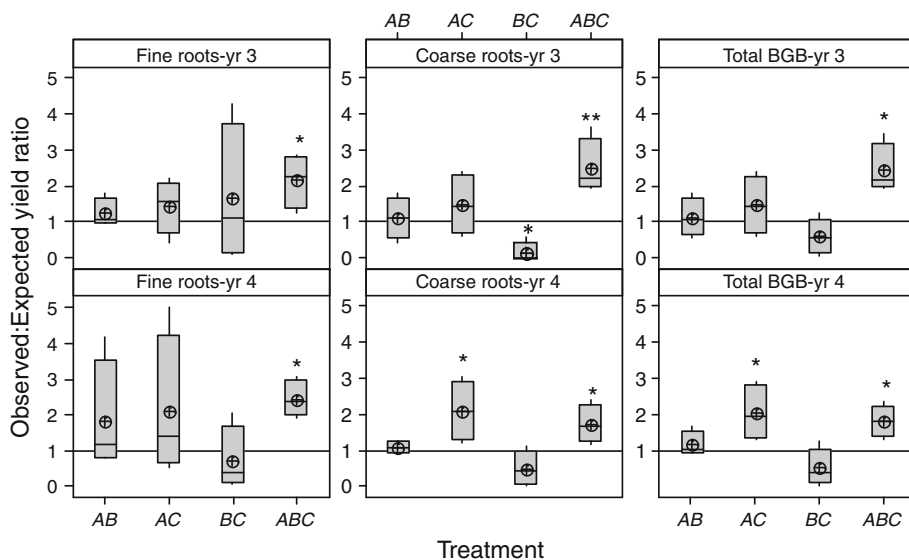
Root profiles

The vertical distributions of root biomass differed significantly between species grown in monocultures; *Avicennia* tended to have a different vertical root distribution compared to *Bruguiera* and *Ceriops*, with a higher proportion of roots in the top part of the soil profile compared with the deeper parts. On the other hand, *Bruguiera* and *Ceriops* had similar rooting traits, with relatively low proportions near the soil surface (Fig. 4; chi-squared analysis for heterogeneity; $\chi^2 = 1,762$, $df = 6$, $P < 0.001$).
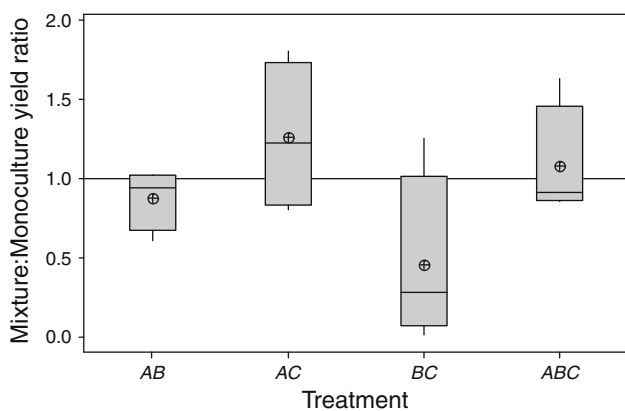

Fig. 3 Transgressive overyielding of mixed mangrove tree species treatments. *Y* values are the ratio of biomass yield from mixed-species plots relative to the yield of the highest yielding monoculture. *Crosses*, *boxes* and *vertical lines* are as defined above in Fig. 2. Mean > 1.0 indicate transgressive overyielding. *Avicennia–Bruguiera* (AB), *Avicennia–Ceriops* (AC) and *Bruguiera–Ceriops* (BC), *Avicennia–Bruguiera–Ceriops* (ABC); $n = 4$ plots/treatments

Discussion

Species identity, and to some extent species richness, enhanced belowground biomass in young mangrove plantations. *Avicennia marina* was the most vigorous species in our experiment; its inclusion had a major influence on the total belowground root biomass, with significant overyielding in two of the mixed-species treatments that contained it. Previous to this study, no work has considered the effects of species mixes on root biomass in mangroves. Brassard et al. (2011) used a comparative rather than experimental approach to demonstrate greater fine root production in mixed- compared with single-species stands of temperate trees. They found evidence for differential use of soil space in mixed stands, suggesting niche complementarity was the mechanism that boosted production. Working in stands with one or two species in British Columbia, Wang et al. (2002) also found that mixed-species stands had higher root densities. We found similar evidence here, with the three species showing differing root profiles: *Avicennia* had a higher proportion of roots in the top compared with the deeper part of the soil profile, whilst
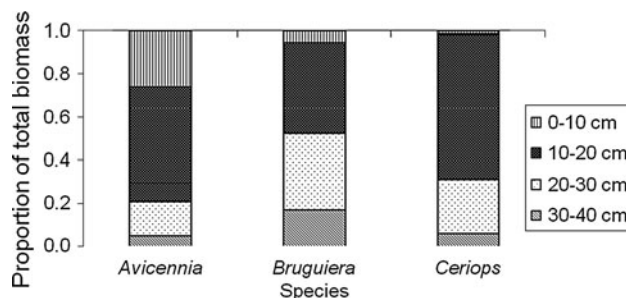

Fig. 4 Vertical distribution of roots in monocultures of young mangrove plantations after three years

Bruguiera and *Ceriops* had similar rooting traits, with relatively low proportions near the soil surface. Mixed stands containing *Avicennia* might therefore show complementary use of niche space and a reduction in belowground competition, leading to the significant overyielding that we observed. Interestingly, the BC mix showed evidence of underyielding in year three, with a significantly lower than expected biomass of coarse roots.

The enhancement of biomass through the inclusion of *Avicennia* was perhaps most clear in the 2008 aboveground biomass data (i.e. after four years), where all treatment mixes that included *Avicennia* were statistically distinct from those that did not. Much of this enhancement effect in mixed treatments is likely to represent a "selection effect" in which the inclusion of a species with a disproportionately strong influence on ecosystem processes drives the experimental responses to biodiversity treatments (Aarssen 1997; Huston 1997; Wardle 1999). *Avicennia* species are usually faster growing than mangroves in the Rhizophoraceae family (Kairo et al. 2001). A formal separation of selection from complementarity effects is not possible here, since we cannot allocate root biomass in mixed plots to individual species (Loreau and Hector 2001). However, positive overyielding provides evidence for complementarity, or perhaps more specifically for "trait-dependent complementarity", in which a species with dominant traits in monoculture shows enhanced yields in mixed plots but without reducing the performance of those species with which it is grown (Fox 2005). Our results are consistent with this; the intraspecific competition that *Avicennia* is likely to suffer belowground due it its vigorous growth and relatively shallow rooting will be diluted by mixing with slower-growing species with different rhizospheres. Other work at the experimental site (Kirui et al. 2008; M. Huxham, unpublished data) has shown no aboveground competitive suppression of *Bruguiera* or *Ceriops* by *Avicennia* in the young mangrove plantations, and the significant overyielding in mixed plots here supports this by showing no evidence for belowground suppression of the less dominant species. However, as the plantations mature, the slower-growing species, *Ceriops* and *Bruguiera*, may suffer suppression from the vigorous *Avicennia*. *Avicennia* species have been shown to have a wide tolerance of environmental conditions, including high salinity and aridity (Tomlinson 1986; Medina and Francisco 1997; Kirui et al. 2008). As a pioneer species, *Avicennia marina* is fit for the harsh conditions at a site which had seen a system shift from a forested area to a sandflat following deforestation ∼30 years ago.

Although *Ceriops* and *Bruguiera* did not suffer reduced production when grown with *Avicennia*, the absence of significant transgressive overyielding effects suggests that they also showed no enhanced growth. Transgressive overyielding would correspond to "trait-independent complementarity" in Fox's terminology (Fox 2005); and would imply either nonoverlapping niches or facilitation. The former is clearly untrue for these species. The latter is possible, but perhaps more likely in older trees. Fargione et al. (2007) showed that selection effects decreased and complementarity effects increased over time in their ten-year experiment with nonwoody plants, as mixed stands became more efficient in their capture and use of nitrogen. Like theirs, our site is nitrogen limited, and nitrogen-mediated intraspecific facilitation has been demonstrated in other mangroves (Kumara et al. 2010). Hence, facilitation may emerge with time in our experiment, but is likely to take longer than with grassland plants.

Root:shoot ratios, and hence belowground investment of trees, increased over time; in year three all treatments had an RSR of ≤1.0, whilst all treatments had an RSR > 1.0 in the fourth year of growth, except for monospecific *Ceriops* plots. The RSR values reported here are comparable to the ranges observed for mangroves elsewhere (0.7–4.1) (Saintilan 1997a, b). High RSR in mangroves have been interpreted as a mechanism for survival in harsh environments; they ensure increased absorption of water and nutrients, as evidenced by positive relationships between salinity and RSR (Saintilan 1997a, b; Hogarth 1999).

Implications of study findings

Brassard et al. (2011) highlight the paucity of studies on biodiversity and ecosystem function that consider belowground effects, particularly in trees, despite roots contributing up to half of annual net primary production in terrestrial forests. The argument for considering belowground processes is even stronger in mangroves, where investment in roots is generally higher than for terrestrial trees, and where root productivity supports ecosystem services that are novel or exceptional. High belowground production, which generates peat and consequent surface elevation, allows mangrove ecosystems to keep pace with sea level rise and thus contribute to coastal protection (McKee et al. 2007; Gilman et al. 2008). In addition, these belowground accumulations of organic material are of global significance as a long-term carbon sink (Donato et al. 2011). Hence, understanding belowground processes in mangroves is of both fundamental and applied interest. Our results suggest that species richness can boost belowground biomass, at least in young plantations, and thus using mixed-species plantations might enhance ecosystem services such as carbon sequestration in mangrove forests.

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