ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Mixing *Eucalyptus* and *Acacia* trees leads to fine root over-yielding and vertical segregation between species

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Abstract The consequences of diversity on belowground processes are still poorly known in tropical forests. The distributions of very fine roots (diameter <1 mm) and fine roots (diameter <3 mm) were studied in a randomized block design close to the harvest age of fast-growing plantations. A replacement series was set up in Brazil with mono-specific *Eucalyptus grandis* (100E) and *Acacia mangium* (100A) stands and a mixture with the same stocking density and 50 % of each species (50A:50E). The total fine root (FR) biomass down to a depth of 2 m was about 27 % higher in 50A:50E than in 100A and 100E. Fine root over-yielding in 50A:50E resulted from a 72 % rise in *E. grandis* fine root biomass per tree relative to 100E, whereas *A. mangium* FR biomass per tree was 17 % lower than in 100A. Mixing *A. mangium* with *E. grandis* trees led to a drop in *A. mangium* FR biomass in the upper 50 cm of soil relative to 100A, partially balanced by a rise in deep soil layers. Our results highlight similarities in the effects of directional resources on leaf and FR distributions in the mixture, with *A. mangium* leaves below the *E. grandis* canopy and a low density of *A. mangium* fine roots in the resource-rich soil layers relative to monospecific stands. The vertical segregation of resource-absorbing organs did not lead to niche complementarity expected to increase the total biomass production.

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Introduction

The role of species diversity in ecosystem functioning is an important issue in functional ecology attracting increasing attention over the last decade. A tendency towards higher production in mixed-species communities than in mono-specific ecosystems (i.e. 'over-yielding') has been documented in grasslands (Tilman et al. 1996; Hector et al. 1999; Marquard et al. 2009) and more recently in forests (e.g. Binkley et al. 2003; Vilà et al. 2003; Forrester et al. 2006; Pretzsch and Schütze 2009; Paquette and Messier 2011). Even though a 'sampling-effect' may have biased some results (Fridley 2001), most of the studies suggest that inter-specific interactions are likely to enhance total biomass production through an increase in resource availability, resource use and/or more efficient use of resources in producing biomass compared to monocultures (Richards

et al. 2010; Cardinale et al. 2011). Two types of interspecific interactions have been proposed to explain the positive effects of biodiversity on productivity: (1) facilitation processes may lead to an increase in the availability of resources for one species due to other species or to modifications in the environment (Callaway 2002), and (2) complementarity between species, including niche differentiation, making it possible to increase the amount of available resources (Fridley 2001; Cardinale et al. 2007). However, other studies have shown no impact or a depressive effect of mixtures on aboveground forest production (e.g. Forrester et al. 2006).

The vast majority of studies investigating the relationships between diversity and productivity in forest ecosystems have been restricted to aboveground tree components (Binkley et al. 2003; Vilà et al. 2003; Kelty 2006; Paquette and Messier 2011). Whilst the influence of a stratified canopy on light interception is well documented (e.g. Bauhus et al. 2004; Hunt et al. 2006), the ability of different species to improve the capture of belowground resources remains unclear (Leuschner et al. 2001; Kelty 2006; Kueffer et al. 2007; Meinen et al. 2009). Studies dealing with fine root densities in mixed-species forest ecosystems are scarce and mainly restricted to the top soil (often 0–30 cm) in boreal and temperate regions. As usually observed for aboveground tree components, an overall trend of fine root over-yielding has been shown in mixed-species forests (e.g. Schmid 2002; Brassard et al. 2011). However, some studies did not detect significant differences between fine root biomasses in mixed- and single-species stands (Bauhus et al. 2000; Meinen et al. 2009; Lei et al. 2012). Size-asymmetric interspecific root competition has been shown in temperate forests (Leuschner et al. 2001; Rewald and Leuschner 2009; Lei et al. 2012). Belowground competition matching aboveground competition can lead to the displacement of the dominated species' fine roots towards soil layers with fewer resources at both nutrient-rich and nutrient-poor sites (Schmid 2002; Schmid and Kazda 2002). Scramble competition (through resource depletion) or contest competition (that inhibits access of other roots to resources through species-specific mechanisms) are likely to affect the development of the competitors' roots in mixed-species stands (Schenk 2006).

The aim of our study was to investigate the effects of interspecific interactions between highly productive tree species on their rooting patterns in deep tropical soils. We used an experiment combining an additive and a replacement series between *Eucalyptus grandis* Hill ex Maid. and *Acacia mangium* (Willd.) trees in southern Brazil (Laclau et al. 2008). Extensive data collection in this experiment showed that aboveground net primary production (ANPP) from planting to harvesting was significantly higher in

monospecific *E. grandis* (100E) than *A. mangium* (100A) stands, with the mixture (50A:50E) in an intermediate position (Nouvellon et al. 2012). Gross primary production of about 4.2 kg C m^{-2} year^{-1} in 100E (Nouvellon et al. 2012) was in the highest range of world forest production (Luyssaert et al. 2007). Higher vertical growth rates for *E. grandis* trees than for *A. mangium* trees led to a stratified canopy in 50A:50E, from 2 years after planting onwards (Laclau et al. 2008). Total belowground carbon fluxes (TBCF) estimated from soil CO_2 efflux measurements over the last 2 years before harvesting showed that belowground carbon (C) allocation was significantly greater in mixed stands than in monospecific plantations (Nouvellon et al. 2012). Silva et al. (2009) showed in the additive series of this experiment that *E. grandis* fine root distributions were not influenced by *A. mangium* trees. By contrast, *A. mangium* fine roots were excluded from the upper soil layer in the mixture with *E. grandis* trees. The conclusions of their study carried out over the early growth period (tree age <2.5 years) were hampered by higher stocking densities in a mixture than in monospecific stands. Our study was carried out in the replacement series of the same experiment (100A, 100E and 50A:50E stands), 1 year before the harvest (5-year-old trees). To our knowledge, it is the first study investigating the effects of interspecific interactions on fine root development close to the harvest age of tropical forests, in replicated treatments manipulating species diversity. Although studies in agroforestry systems have shown that trees and crops can explore deep soil layers differently (Lehmann 2003; Allen et al. 2004; Mulia and Dupraz 2006), the effects of species mixing on root distributions below a depth of 1 m are little documented in mixed-species forests. We put forward the hypotheses that: (1) mixing *E. grandis* and *A. mangium* trees significantly increases fine root biomass down to a depth of 2 m in comparison with single-species stands (transgressive over-yielding hypothesis), as suggested by TBCF estimations, and (2) interspecific interactions in mixed-species stands lead to the exclusion of *A. mangium* roots from the soil layer with the highest availability of water and nutrients, which matches the superiority of *Eucalyptus* in aboveground competition (competitive exclusion hypothesis; Schenk 2006).

Materials and methods

Study site

The study was carried out at the Itatinga Experimental Station (University of São Paulo) located at 23°02′S, 48°38′W. The long-term average rainfall from 1990 to 2010 was 1,390 mm with a cold season from June to

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September. The average annual temperature was 19 °C with minimum temperature values below 5 °C for a few days each year.

The experiment was located on a hilltop (slope <3 %) 860 m above sea level. The soils were Ferralsols according to the FAO classification developed on cretaceous sandstone. Textural uniformity was high (clay content around 15 %). The pH was acidic (about 5.5) and the amounts of bioavailable nutrients in this soil were low. Effective cation exchange capacity ranged from 0.2 to 1.8 $cmol_c kg^{-1}$ in the upper 3 m of soil and the amounts of exchangeable base cations (K^+, Na^+, Ca^{2+}, Mg^{2+}) were <0.1 $cmol_c kg^{-1}$ beyond a depth of 5 cm (Table 1).

The experiment was set up in a former *Eucalyptus saligna* Sm. plot managed as a coppice without fertiliser applications from 1940 to 1998. The stumps were killed by glyphosate application and *E. grandis* seedlings were planted in 1998 with low fertilizer inputs (30, 26 and 25 kg ha^{-1} of N, P and K, respectively). Only the boles of the *E. grandis* stand were harvested in December 2002 and harvest residues were spread uniformly in the field.

Experimental layout

A complete randomized block design was set up in May 2003 with seven treatments and four blocks in order to assess the influence of *A. mangium* trees on the growth of *E. grandis* seedlings. Each plot had a total area of 30 × 30 m and an inner plot of 18 × 18 m with two buffer rows. A complete description of the experimental layout can be found in Laclau et al. (2008). Our study was carried out in three treatments and three blocks:

– 100A, monospecific *A. mangium* stand;
– 100E, monospecific *E. grandis* stand;
– 50A:50E, mixture in a proportion of 1:1 between *E. grandis* and *A. mangium* trees.

The seedlings were planted at a spacing of 3 × 3 m after cultivation with a ripping tine down to a depth of 40 cm, without N fertilisation. *Acacia mangium* seedlings were inoculated with *Rhizobium* strains selected for their N$_2$ fixation capacities. In the 50A:50E treatment, the two species were planted alternately in the row, and between adjacent rows (Fig. 1). Two tons per hectare of dolomitic limestone were applied at planting and 40 g P plant^{-1} were buried 20 cm from the plants, as well as 9 g K plant^{-1}, 3 g B plant^{-1}, 6 g Fe plant^{-1}, 3 g Zn plant^{-1}, and 1 g Mn plant^{-1}. Three complementary fertilisations were applied with 25 kg K ha^{-1} at 6, 12 and 18 months after planting in the three treatments. Another treatment with a total application of 120 kg ha^{-1} of N (ammonitrate fertiliser) in monospecific *E. grandis* stands in this experiment showed that N fertilisation significantly enhanced tree growth in the

Table 1 Main soil characteristics in the experiment

Soil layer (cm)	Particle size distribution (%)			pH (H$_2$O)	Total C g kg^{-1}	Total N g kg^{-1}	P resin (mg kg^{-1})	Exchangeable cations (cmol$_c$ kg^{-1})					
	Clay	Silt	Sand					Ca	Mg	K	Na	Al	CEC
0–5	11.4 (0.7)	4.1 (0.7)	84.5 (0.9)	5.5 (0.2)	17.6 (3.8)	0.9 (0.2)	4.0 (0.4)	0.464 (0.096)	0.424 (0.035)	0.017 (0.004)	0.015 (0.011)	0.581 (0.133)	1.758 (0.274)
5–15	12.8 (0.7)	3.1 (0.3)	84.1 (0.7)	5.5 (0.1)	6.4 (0.7)	0.3 (0.2)	2.5 (0.2)	0.018 (0.002)	0.063 (0.003)	0.006 (0.001)	0.005 (0.005)	0.643 (0.018)	0.947 (0.023)
15–50	14 (0.7)	3.2 (0.4)	83.7 (0.4)	5.4 (0.1)	5.0 (0.4)	0.4 (0.0)	1.9 (0.2)	0.003 (0.001)	0.018 (0.003)	0.005 (0.002)	0.003 (0.002)	0.554 (0.021)	0.751 (0.025)
50–100	16.1 (0.0)	3.4 (0.2)	80.5 (0.2)	5.8 (0.3)	3.5 (0.1)	0.2 (0.0)	1.3 (0.2)	0.002 (0.001)	0.005 (0.000)	0.001 (0.000)	0.000 (0.000)	0.405 (0.017)	0.584 (0.012)
100–200	18.1 (0.0)	4.1 (0.2)	77.8 (0.2)	5.9 (0.0)	2.6 (0.1)	0.2 (0.0)	1.2 (0.0)	0.002 (0.001)	0.008 (0.001)	0.002 (0.000)	0.001 (0.001)	0.299 (0.030)	0.436 (0.029)
200–300	16.1 (0.0)	4.4 (0.8)	79.5 (0.8)	5.7 (0.1)	2.1 (0.1)	0.1 (0.0)	2.0 (0.2)	0.003 (0.003)	0.006 (0.001)	0.000 (0.000)	0.002 (0.001)	0.136 (0.011)	0.211 (0.037)

Standard errors are given in parentheses (n = 3). Soils were sampled down to a depth of 3 m, 3 years after treatment establishment, in one pit in each treatment (100A, 100E and 50A:50E) in block 1

first 2 years after planting, but aboveground biomass was no longer significantly affected by N fertiliser addition at age 3 years (Laclau et al. 2008).
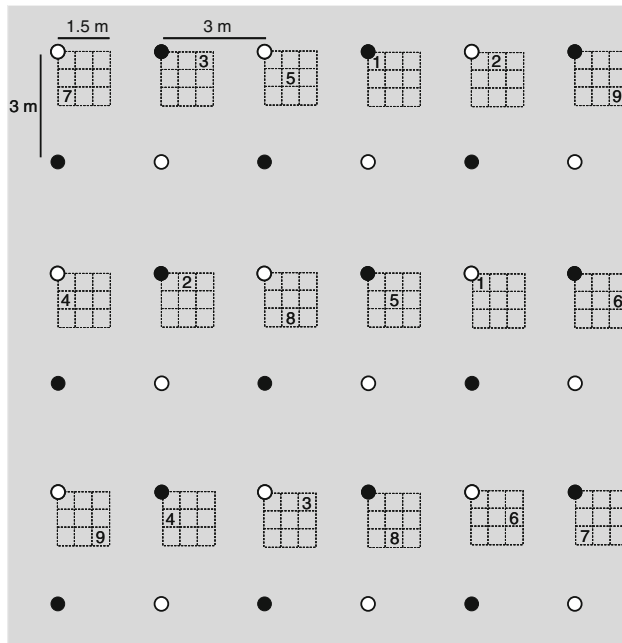

Fig. 1 Sampling positions in the 50A:50E treatment. In each inner plot (excluding two buffer rows), nine positions were randomly sampled close to *Acacia* trees (*full circle*) and nine positions close to *Eucalyptus* trees (*open circle*). The same design was used in treatments 100A and 100E with nine positions per plot. The centres of the nine squares (0.5 × 0.5 m) were sampled for each species

Our study was carried out 5 years after planting. At this age, the stocking density of living trees was similar in the three treatments (about 1,100 trees per hectare) and *E. grandis* tree height was 10–12 m higher than *A. mangium* tree height in single- and mixed-species stands (Table 2). Mixing the two species led to slight aboveground over-yielding with 6 % more total aboveground biomass in 50A:50E than the average of the two single-species stands. However, the aboveground biomass at age 5 years was 11 % lower in 50A:50E than in 100E. A detailed description of the dynamics of biomass accumulation within tree components over the full rotation is given by Nouvellon et al. (2012).

Root sampling

Fine roots <3 mm in diameter were sampled down to a depth of 2 m in the three treatments (100A, 100E and 50A:50E) and three blocks. Two root classes were distinguished within each sample: very fine roots <1 mm in diameter (FR1) and roots with a diameter between 1 and 3 mm (FR1-3). We used a threshold of 3 mm to allow comparisons of fine root mass with previous studies in *E. grandis* and *A. mangium* plantations at our study site (Silva et al. 2009). A further separation of fine roots smaller than 1 mm diameter was carried out to study the development of the roots directly involved in the physiological processes of water and nutrient uptake. Nine positions per plot were sampled in the single-species treatments

Table 2 Main characteristics of the stands at 5 years of age

| | 100A | 100E | 50A:50E | | |
	A. mangium	*E. grandis*	*A. mangium*	*E. grandis*	Total
Stocking density (trees ha^{-1})	1,069.9 ± 20.6	1,111.0 ± 0.0	555.5 ± 0.0	534.9 ± 20.6	1,090.4 ± 10.3
Stand basal area (m^2 ha^{-1})	20.8 ± 1.0	20.8 ± 0.2	5.8 ± 0.3	14.8 ± 0.7	20.6 ± 0.6
Tree height (m)	13.4 ± 0.3	23.0 ± 0.3	11.5 ± 0.1	23.5 ± 0.7	17.6 ± 0.3
Biomass (kg m^{-2}):					
Leaves	0.50 ± 0.04	0.61 ± 0.01	0.19 ± 0.01	0.53 ± 0.05	0.72 ± 0.04
Branches	1.69 ± 0.10	1.06 ± 0.02	0.37 ± 0.02	1.14 ± 0.08	1.52 ± 0.07
Trunks	5.62 ± 0.32	9.71 ± 0.21	1.32 ± 0.06	6.57 ± 0.38	7.90 ± 0.34
Coarse[a] roots	0.95 ± 0.06	2.18 ± 0.05	0.27 ± 0.00	1.64 ± 0.12	1.92 ± 0.12
Medium-sized[b] roots	0.13 ± 0.01	0.22 ± 0.00	0.04 ± 0.00	0.19 ± 0.00	0.23 ± 0.00
Fine[c] roots (our study)	0.35 ± 0.02	0.35 ± 0.05	0.15 ± 0.01	0.29 ± 0.01	0.44 ± 0.01
Aboveground biomass	7.81 ± 0.45	11.37 ± 0.24	1.89 ± 0.09	8.25 ± 0.51	10.14 ± 0.44
Belowground biomass	1.44 ± 0.05	2.74 ± 0.05	0.46 ± 0.01	2.13 ± 0.14	2.59 ± 0.13
Total stand biomass	9.25 ± 0.50	14.11 ± 0.27	2.35 ± 0.09	10.37 ± 0.65	12.73 ± 0.57
Fine root/total biomass	0.038 ± 0.004	0.025 ± 0.004	0.064 ± 0.002	0.028 ± 0.001	0.035 ± 0.001

Standard errors between the blocks are indicated ($n = 3$). A complete description of the methods used is given in Nouvellon et al. (2012)

[a] Root diameter >10 mm

[b] Root diameter between 10 and 3 mm

[c] Root diameter <3 mm

(100A and 100E) and 18 positions in 50A:50E (Fig. 1). Cores were taken with a steel soil corer driven into the soil by a sledgehammer. We used a soil corer with an internal diameter of 8 cm down to a depth of 50 cm and another soil corer with an internal diameter of 4.5 cm between 50 and 200 cm. Cores were sampled stepwise to avoid soil compaction, at the following depths: 0–10, 10–30, 30–50, 50–100, 100–150 and 150–200 cm.

All the roots of each species were washed free of soil and separated carefully (sight, touch and flotation if required) into living roots and dead roots. Dead roots were discarded and only live rootlets were studied. Whilst living roots were pale and pliable, dead roots were breakable and dark. Living roots were sorted according to various criteria such as living stele, bright colour and elasticity. The colour of the roots was a good indication of the species to which they belonged. Reference roots sampled in monospecific stands were used to facilitate the identification of each species for roots collected in the 50A:50E treatment. *Eucalyptus grandis* fine roots had a higher branching proportion and were darker than *A. mangium* fine roots. The samples of each component were dried at 65 °C to constant weight. After carefully removing the last adherent soil particles by hand, samples were weighed ($\pm$0.0001 g). Root densities were calculated by dividing the dry matter of roots by the volume of the soil sample. Biomasses of FR1 and FR1-3 were computed in each soil layer multiplying the volume of the layer by the mean density of roots <1 mm in diameter, and with a diameter between 1 and 3 mm, respectively.

Soil water contents

A pit was dug manually down to a depth of 3.0 m at the centre of the 100A and 100E plots of block 1, 2.5 years after planting. Three TDR probes (Trase; Soilmoisture, Santa Barbara, USA) were horizontally buried at depths of 0.15, 1.50 and 3.0 m (9 probes per plot) in an undisturbed area at different distances from trees. The trenches were back-filled with soil horizons in their natural arrangement after installation. Probe calibration was checked by gravimetric soil water content and bulk density measurements. Volumetric soil water contents were measured every 1–2 weeks from September 2005 to April 2008 (except during periods of equipment failure).

Data analyses

Sampling positions were located close to different trees in each plot and individual root biomass measurements within a given soil layer were thus considered independent. Three-way analyses of variance (ANOVAs) were used to test the effects of treatments, blocks, and sampling positions, as well as the interaction between positions and treatments on total FR1 and FR1-3 densities (irrespective of the species) in each soil layer (0–10, 10–30, 30–50, 50–100, 100–150, 150–200 and 0–200 cm). Root densities of each species in 50A:50E were compared with 50 % of the root density at the same spatial position in the monoculture of the same species, to test the effects of interspecific interactions on root densities. The main factors of the ANOVAs were treatment, block, sampling position (from 1 to 9), species of the closest tree (see Fig. 1) and the interactions between species of the closest tree and sampling positions, as well as between treatments and sampling positions. A residual analysis was performed to check whether the residuals met the assumptions of the ANOVA and, if necessary, raw data were log- or square root-transformed so that residuals were homoscedastic and normally distributed. The probability level used to determine significance was $P < 0.05$. When significant differences were detected between treatment levels, the Bonferroni multiple range test was used to compare treatment means. Pearson correlation coefficients between root densities in each soil layer, and the distance from the nearest trunk of each species, were computed for each treatment. All the data were processed using the software package SAS v.9.2 (SAS, Cary, NC, USA).

Results

Dynamics of soil water content

Soil water contents during the dry season were about 50 % higher in 100A than in 100E at depths of 150 and 300 cm the third year after planting (Fig. 2). Even though differences between the two monocultures declined as stands developed, the time-course of soil water contents showed lower amounts of water withdrawn from the upper 3 m of soil in 100A than in 100E. Whilst gravitational solutions transferred in deep soil layers by drainage only reached 3 m in depth three times from 2.5 to 5 years after planting in 100E, and during very short periods, nine increases in soil water contents occurred at a depth of 3 m in 100A.

Fine root over-yielding

Mixing *A. mangium* trees with *E. grandis* trees led to a 27–28 % higher total FR biomass (diameter <3 mm) down to a depth of 2 m in 50A:50E than in 100A and 100E. Total FR1 biomass was 269.2, 239.4 and 302.3 g m^{-2} in 100A, 100E and 50A:50E, respectively (Table 3), and FR1-3 biomass was 82.8, 107.5 and 143.0 g m^{-2} in 100A, 100E and 50A:50E, respectively (Table 4). FR1 comprised 68–76 % of the biomass of total fine roots in the three treatments. Mean FR1 density in the 0–2 m soil layer was
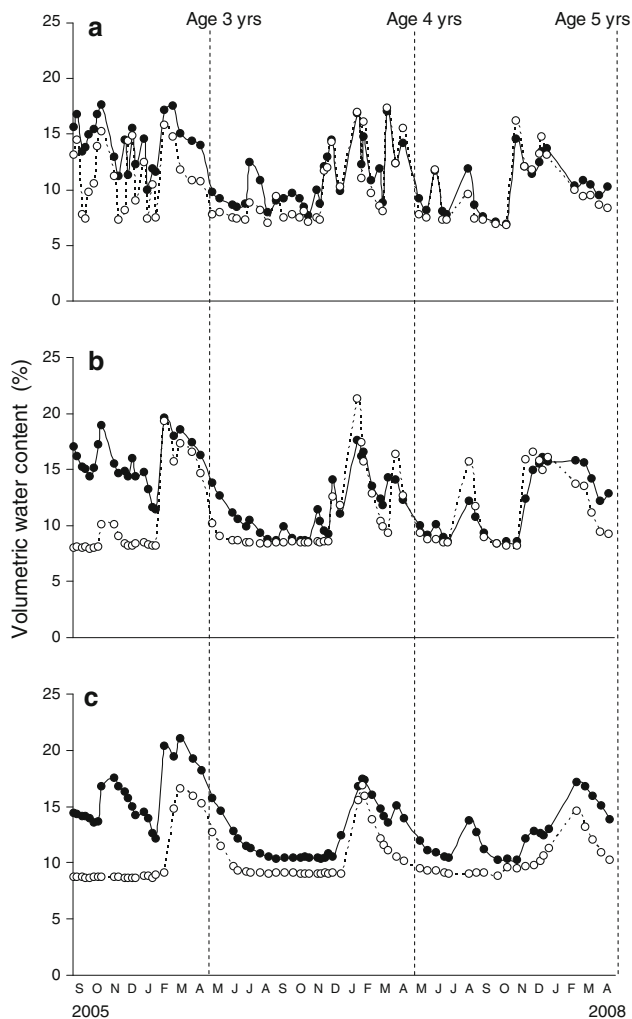
Fig. 2 Dynamics of volumetric soil water contents at depths of 15 cm (a), 150 cm (b) and 300 cm (c) in 100A (*filled symbols*) and 100E (*open symbols*) from 2.5 to 5 years after planting

significantly higher close to trees (position 1) than far from trees (position 9), but spatial positions did not significantly influence the FR1-3 density (data not shown). The interaction between position and treatment was not significant, whatever the diameter class.

Fine root density distributions down to a depth of 2 m exhibited different patterns of soil space occupation in the three treatments (Fig. 3). A tendency towards higher fine root densities in 50A:50E than in 100A was found at depths >50 cm, but the differences were only significant for FR1-3. Fine root over-yielding in 50A:50E relative to 100E was a result of 20–100 % higher root densities in all the soil layers (except the 0–10 cm layer for FR1-3). Only soil layers at depths >50 cm were involved in fine root over-yielding in 50A:50E relative to 100A (Fig. 3). Fine root over-yielding in the mixture relative to monospecific *A. mangium* stands was accounted for by 25-63 % higher FR1 densities in 50A:50E, along with FR1-3 densities that were more than double those in 100A in the 50–100, 100–150 and 150–200 cm soil layers.

Root distributions of each species in a mixture vs. monocultures

Comparisons of fine root vertical distributions for each species in 50A:50E and in monospecific stands showed that fine root development was largely affected by intra- and interspecific interactions. For a stocking density of *A. mangium* and *E. grandis* trees that was 50 % lower in 50A:50E than in single-species stands, the *A. mangium* fine root biomass cumulated down to a depth of 2 m in 50A:50E amounted to 46 and 33 % of the amounts in 100A for FR1 and FR1-3, respectively, and the *E. grandis* fine root biomass in 50A:50E was 75 % and 108 % of the amounts in 100E for FR1 and FR1-3, respectively (Tables 3, 4). *Eucalyptus grandis* FR1 biomass in 50A:50E was significantly more than 50 % of the biomass in 100E for the 10–30 and 30–50 cm soil layers (Fig. 4a). The same pattern was found for *E. grandis* FR1-3 biomass in the 50–100 and 100–150 cm soil layers (Fig. 4b), and the trend was similar for the two classes of fine roots in other soil

Table 3 Biomass (g m^{-2}) of roots <1 mm in diameter down to a depth of 2 m in the 100A, 100E and 50A:50E treatments

| Soil layer (cm)	100A *A.m.* roots	100E *E.g.* roots	50A:50E		
			A.m. roots	*E.g.* roots	Total root mass
0–10	84.1 a (31 %)	53.9 b (23 %)	28.8 (23 %)	35.2 (20 %)	64.0 ab (21 %)
10–30	35.2 ab (13 %)	30.5 b (13 %)	15.9 (13 %)	24.4 (14 %)	40.3 a (13 %)
30–50	24.4 a (9 %)	16.0 b (7 %)	5.7 (5 %)	17.1 (10 %)	22.8 ab (8 %)
50–100	43.5 a (16 %)	41.4 a (17 %)	19.0 (15 %)	39.3 (22 %)	58.4 a (19 %)
100–150	43.7 a (16 %)	45.7 a (19 %)	27.5 (22 %)	27.0 (15 %)	54.5 a (18 %)
150–200	38.2 a (14 %)	52.0 a (22 %)	26.9 (22 %)	35.5 (20 %)	62.3 a (21 %)
Total	269.2 ab (100 %)	239.4 b (100 %)	123.8 (100 %)	178.5 (100 %)	302.3 a (100 %)

The percentage of root mass in each soil layer relative to the total amount in the 0–2 m soil layer is indicated in parentheses. Different letters in the same row indicate significant differences ($P < 0.05$) between total root biomasses in the 100A, 100E and 50A:50E treatments

Table 4 Biomass (g m^{-2}) of roots between 1 and 3 mm in diameter down to a depth of 2 m in treatments 100A, 100E and 50A:50E

Soil layer (cm)	100A *A.m.* roots	100E *E.g.* roots	50A:50E		
			A.m. roots	*E.g.* roots	Total root mass
0–10	14.1 a (17 %)	20.9 a (19 %)	2.4 (9 %)	17.5 (15 %)	19.9 a (14 %)
10–30	27.1 a (33 %)	13.9 a (13 %)	5.2 (19 %)	13.8 (12 %)	19.0 a (13 %)
30–50	4.3 a (5 %)	8.0 a (7 %)	0.5 (2 %)	8.1 (7 %)	8.5 a (6 %)
50–100	13.4 b (16 %)	20.7 ab (19 %)	4.4 (16 %)	23.9 (21 %)	28.4 a (20 %)
100–150	13.3 b (16 %)	21.8 ab (20 %)	6.4 (23 %)	28.6 (25 %)	35.0 a (24 %)
150–200	10.6 b (13 %)	22.2 ab (21 %)	8.5 (31 %)	23.6 (20 %)	32.1 a (22 %)
Total	82.8 b (100 %)	107.5 b (100 %)	27.4 (100 %)	115.6 (100 %)	143.0 a (100 %)

The percentage of root mass in each soil layer relative to the total amount in the 0–2 m soil layer is indicated in parentheses. Different letters in the same row indicate significant differences ($P < 0.05$) between total root biomasses in the 100A, 100E and 50A:50E treatments

Fig. 3 Mean densities of fine roots <1 mm in diameter (**a**) and between 1 and 3 mm in diameter (**b**) down to a depth of 2 m in treatments 100A (*filled black bars*), 100E (*open bars*) and 50A:50E (*filled grey bars*, irrespective of species). Standard errors between blocks are indicated ($n = 3$). When differences between treatments were significant in the same soil layer ($P < 0.05$), they are indicated by *different letters*
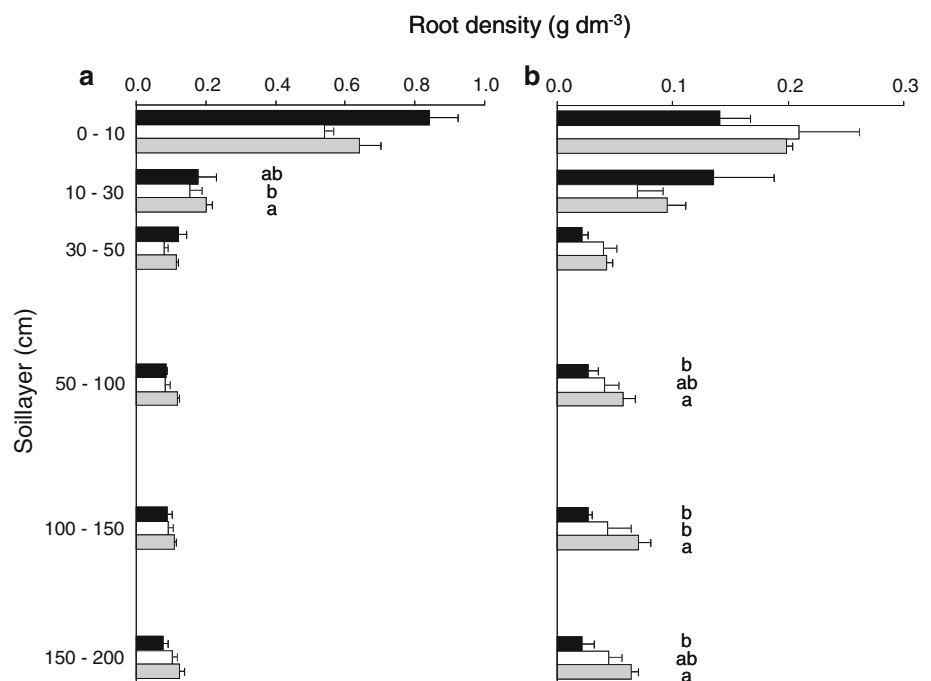
layers even though the differences were not significant. Mixing *A. mangium* with *E. grandis* trees led to a drop in *A. mangium* fine root biomass in the upper 50 cm of soil relative to 100A, roughly balanced by a rise in deep soil layers. However, *A. mangium* FR densities in 50A:50E were only significantly lower than 50 % of the values in 100A in the 0–10 and 30–50 cm soil layers (both for FR1 and FR1-3).

Acacia mangium and *E. grandis* fine root distributions did not exhibit a clear pattern of horizontal soil exploration. Fine root densities of the two species were not significantly correlated with the distance from trees whatever the soil layer (except in the 30–50 cm layer for *A. mangium* roots), in mixed- and single-species stands. The sampling position effect was not significant in the ANOVAs performed between *A. mangium* fine root densities in 50A:50E and

50 % of the densities in 100A for most of the soil layers. Mixing *E. grandis* with *A. mangium* trees did not significantly modify the densities of *E. grandis* FRs at the sampled positions, whatever the soil layer. Neither *A. mangium* nor *E. grandis* FR1 were totally excluded from any soil layer in the mixture, whatever the sampled distances from each tree species (data not shown).

Discussion

Fine root over-yielding

In agreement with our first hypothesis, mixing *A. mangium* with *E. grandis* trees led to transgressive over-yielding in FR biomass close to the harvest age. It exclusively resulted
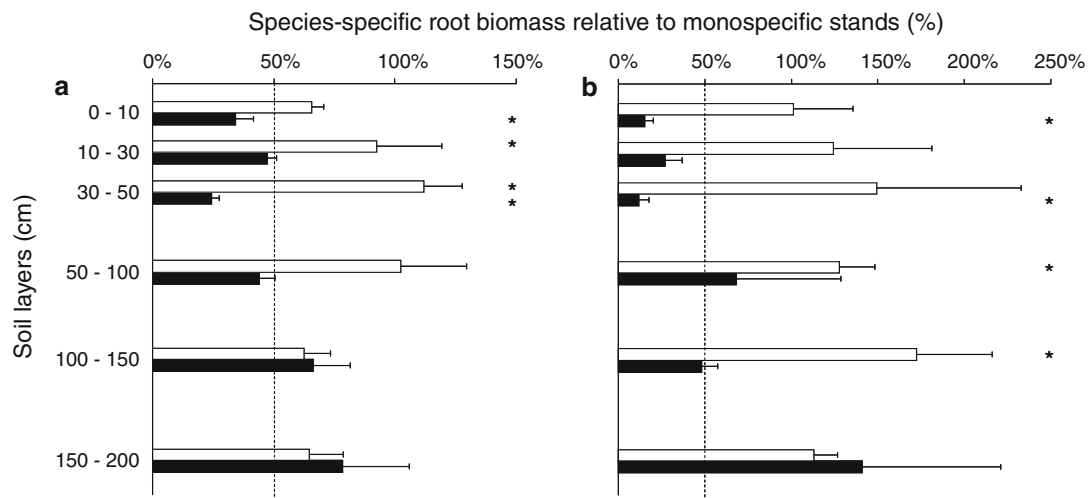
Species-specific root biomass relative to monospecific stands (%)

Fig. 4 Percentages of FR1 biomass (<1 mm in diameter) (**a**), and FR1-3 biomass (diameter 1–3 mm) (**b**), in the 50A:50E treatment relative to the amounts in each soil layer for the single-species stands. The *dotted line* indicates the percentage expected for *Eucalyptus* roots (*open bars*) and *Acacia* roots (*filled bars*) if root development was similar to that in monospecific stands (with a half stocking density for each species). Standard errors between the three blocks are indicated and * denotes a significant difference ($P < 0.05$) between the root biomass of a particular species in 50A:50E and 50 % of the biomass at the same positions in the pure stands of the same species

from a sharp increase in *E. grandis* fine root densities, since the total *A. mangium* fine root biomass down to a depth of 2 m in 50A:50E was slightly less than 50 % of the biomass in 100A. Transgressive over-yielding in our 5-year-old mixture was consistent with TBCF from 4 to 6 years after planting, which was significantly higher in 50A:50E (1.13 g C m^{-2} year^{-1}) than the mean between 100E and 100A (0.94 g C m^{-2} year^{-1}) (Nouvellon et al. 2012). Even though a large share of TBCF is allocated to fine root production, respiration, exudation and to mycorrhiza (Maier et al. 2004; Cairney 2012), fine root respiration contributes to 30–55 % of total soil CO_2 effluxes in tropical *Eucalyptus* plantations (Nouvellon et al. 2008; Marsden et al. 2008). Consequently, the larger fine root biomass in 50A:50E than in single-species stands probably contributed to the differences in TBCF between stands. Higher fine root biomass and fine root production in mixed-species stands than in single-species stands were also shown in *Pinus taeda* L. and *Robinia pseudoacacia* L. plantations (Fredericksen and Zedaker 1995) and in forests with *Populus tremuloides* Michx. trees in two boreal regions (Brassard et al. 2011). Likewise, FR over-yielding was reported in mixed-species forests of *Tsuga heterophylla* (Raf.) Sarg. and *Thuja plicata* Donn. ex D. Don stands (Wang et al. 2002), as well as in *Fagus sylvatica* L. and *Picea abies* (L.) Karst. stands at both nutrient-rich and nutrient-poor sites (Schmid and Kazda 2002). However, other studies did not find significant differences in FR biomass between single- and mixed-species forests down to a depth of 30–40 cm. Fine root biomass in a mixture of *Eucalyptus globulus* Labill. and *Acacia mearnsii* de Wild was similar to monospecific plantations despite transgressive over-

yielding above ground (Bauhus et al. 2000), and similar FR densities were also found in 12 temperate deciduous forests representing a gradient in tree species mixing in central Europe (Meinen et al. 2009). Further investigations are needed to disentangle the effects of contrasting rooting traits (in particular growth and turnover rates) between co-existing species and biotic/abiotic factors on FR over-yielding in mixed-species forests.

Consequences of directional resources on soil space occupation

Rainfall and fertiliser applications in the top soil led to a strong vertical gradient of water and nutrient availabilities in our experiment. Most of the available nutrients are located in the upper soil layer in plantation forests established on highly weathered soils (released by fertilisers over the early growth period and throughout the biological cycle of nutrients after canopy closure) and carried by gravitational solutions (Lilienfein et al. 2000; Laclau et al. 2003, 2010). Soil coring showed that the depth of the water table was about 16 m in our experiment (Christina et al. 2010). Soil water content monitoring, as well as sap flow and eddy covariance measurements in nearby *E. grandis* stands, showed that the total annual rainfall was evapotranspired from the third year after planting onwards and the amount of available water stored in deep soil layers after clear-cutting had already been taken up close to the harvest age (Laclau et al. 2010; Nouvellon et al. 2011). The same pattern probably occurred in the 50A:50E plots where leaf and fine root biomasses were higher than in 100E (Table 2), as reported in another eucalypt and acacia

mixture experiment in Australia (Forrester et al. 2010). Experiments manipulating water and nutrient availabilities in Brazilian *Eucalyptus* plantations under similar environments confirmed that tree growth was limited by water availability in the last years before harvesting (Stape et al. 2010). Consequently, the downward fluxes of water and nutrients after rainfall events led to a strong competitive advantage for trees with the highest density of superficial roots. The capacity to take up gravitational solutions in the top soil rapidly after rainfall events was thus probably a key component of inter-tree competition driving fine root distributions in our experiment.

The strong vertical directional component of natural resources might account for a similar behaviour of the two species aboveground for light capture, and belowground for water and nutrient uptake. Despite a 50 % lower *E. grandis* stocking density in 50A:50E than in 100E, branch biomass at age 2.5 years (Laclau et al. 2008) and fine root densities in most soil layers (present study) for this species were not significantly different between the two treatments. This feature, as well as only a 21 % lower total area of *E. grandis* leaves in 50A:50E than in 100E over the whole rotation (le Maire et al. 2012), suggested a similar behaviour of space occupation above- and belowground for the dominant species in the mixture. Interspecific competition with *A. mangium* trees was weak for *E. grandis* trees which exhibited strong plasticity making it possible to develop almost the same biomass of absorbing organs (leaves and fine roots) as in monocultures, despite a half stocking density. By contrast, crown development in the *A. mangium* trees below the *E. grandis* canopy to capture light (le Maire et al. 2012), as well as the rise in fine root density in deep soil layers offsetting their partial exclusion in the top soil, were greatly influenced by interspecific competition. This pattern shows that *A. mangium* trees grew using natural resources that *E. grandis* trees had not used above ground (i.e. light) or that they had not the capacity to take up rapidly in the upper soil layers (i.e. water and nutrients). A modelling approach showed that mean light use efficiency (ratio of stem biomass increment divided by absorbed photosynthetically active radiation) over the full rotation in our plots was significantly correlated with tree height for *A. mangium* trees but not for *E. grandis* trees, in both single- and mixed-species plots (le Maire et al. 2012). This pattern suggests size-symmetric access to soil resources for *E. grandis* trees in both monospecific plots and in a mixture. By contrast, the positive correlation between *A. mangium* tree height and light use efficiency over the rotation suggests that the tallest *Acacia* trees captured proportionally more soil resources than small *Acacia* trees, leading to more efficient use of the absorbed photosynthetically active radiations. This feature might be explained by a predominance of *A. mangium* roots belonging to the tallest trees in the upper soil layer where the water and nutrient availabilities were highest. Our results thus support the analogy between root competitions for soil resources with a directional component and shoot competition for directional light reported in other studies (Schenk 2006).

Belowground competitive exclusion

Even though the results were in agreement with our second hypothesis, the dominated species' fine roots were only partially excluded from the resource-rich upper soil layer and the shift of *A. mangium* fine roots to deeper layers might also result from an earlier occupation of surface soil horizons by *E. grandis* fine roots. Future experiments are needed to disentangle the causes of fine root stratification in mixed plantations of *A. mangium* and *E. grandis*. In particular, root growth chamber experiments (Leuschner et al. 2001) might be useful to investigate competition between tree fine roots experimentally in the field.

Our systematic soil sampling representative of all the distances from the two tree species in 50A:50E showed a broad overlap of the root systems of neighbouring trees. The lack of significant influence of the distance from trees on the fine root densities of each species in the mixture suggests that competition was less than in mixed plantations of the same species with a double stocking density of *Eucalyptus* trees (Silva et al. 2009). Studies of fine root distributions in agroforestry systems have shown that tree root systems can turn downwards in the presence of herbaceous crops and interspecific interactions can lead to inverted root profiles (Lehmann et al. 1998; Moreno et al. 2005; Mulia and Dupraz 2006). However, this trend might depend on the availability of water and nutrients in deep soil layers. The competitiveness of beech in mixtures has been reported to push the root system of other species towards the surface, with fine roots of beech occupying a large proportion of the deep soil layers when water availability was limiting tree growth during the summer (Schmid 2002; Schume et al. 2004). Studies in agroforestry systems and forest ecosystems therefore suggest that roots of the weakest competitor can be partially excluded from soil areas where the resources limiting tree growth are concentrated. Whilst belowground competition may be considered to decrease when soil resource availability increases (Newman 1973; Coomes and Grubb 2000), the contrasting root distributions for the same species growing in mixed- and single-species stands in our study suggest high levels of competition. These fast-growing plantations require large amounts of water and nutrients throughout their development (Cabral et al. 2010; Laclau et al. 2010; Stape et al. 2010). The lack of aboveground transgressive over-yielding in our mixed plantations suggests that

facilitation processes were limited in comparison with interspecific competition, which followed the general trend of competition dominating over facilitation in environments with high biomass production (Warren et al. 2009; Paquette and Messier 2011).

Further research will be needed to gain insight into the effects of interspecific interactions on mycorrhizal status, FR architecture and FR development down to the root front for the two species. Such studies should be carried out in areas highly depleted in N, where a mixture with N-fixing trees should improve the growth of non-N-fixing trees through complementarity and facilitation mechanisms. Stable isotopes or analogues of nutrients would be useful for comparing root activities in different soil layers for trees in single- and mixed-species stands (Silva et al. 2011). They might be used to quantify the uptake of water and nutrients for each species, which would help to provide insight into the effects of species mixing on size-(a)symmetric competition in tropical forests.

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