



Partitioning of net primary production in *Eucalyptus* and *Acacia* stands and in mixed-species plantations: Two case-studies in contrasting tropical environments

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ABSTRACT

The introduction of nitrogen fixing species (NFS) in fast-growing tree plantations is an alternative option to reduce fertilizer inputs. However, the success of mixed-species plantations depends on the balance between positive interactions among species (resulting from facilitation and/or complementarity) and the negative effects of interspecific competition.

Using a carbon budget approach and coupling measurements of standing biomass, aboveground litter-fall and soil CO₂ efflux, we assessed the influence of replacing half of eucalypt trees by *Acacia mangium* on total belowground carbon flux (TBCF), net primary production (NPP) and its partitioning between above- and belowground growth at two tropical sites in Brazil (Itatinga) and in Congo (Kissoko) exhibiting contrasting climates, edaphic conditions and wood productions.

Annual soil CO₂ efflux (F_S) was significantly lower in the acacia monocultures than in eucalypt monocultures and mixed-species stands at both sites. Annual F_S was significantly lower at Itatinga compared to Kissoko for all stands while TBCF was significantly lower in the eucalypt stands only. In the eucalypt monocultures we found a significantly lower aboveground NPP (ANPP) and wood production (wood NPP) at Kissoko compared to Itatinga that was almost fully balanced by a significantly higher belowground NPP (BNPP), leading to similar NPP. Similarly, acacia monocultures exhibited significantly higher ANPP and wood NPP at Itatinga than at Kissoko. The mixed-species stands exhibited a significantly lower wood NPP and ANPP than the eucalypt monocultures at the Brazilian site while NPP of the mixture was not significantly different than the average NPP of the two monocultures. At the Congolese site, NPP of the mixture was significantly higher than the average NPP of the two monocultures. NPP was similar in the mixed-species stand and the eucalypt monoculture with a significantly lower partitioning of NPP to belowground production, leading to a one third higher wood biomass at harvest in the mixed-species stand.

A positive effect of growing eucalypts with the nitrogen fixing acacia trees on stand wood production occurred at Kissoko but not at Itatinga. Mixed-species plantations with NFS can be advocated at sites where the productive gains resulting from nitrogen fixation are not compromised by other resource limitations.

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1. Introduction

According to the Millennium Ecosystem Assessment, forest plantations represent only 5% of total forest area, but they fulfill more than one third of the world demand for wood products, an amount anticipated to increase sharply in the next decades (Sampson et al., 2005). Eucalypt (*Eucalyptus* sp.) is the most widely

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planted hardwood genus in the tropics, offering high productivity on short-term rotations even on weathered, nutrient poor soils. However, the large nutrient demand of eucalypt plantations and the large amount of nutrients exported at the end of each rotation raise questions about the sustainability of the intensive eucalypt silviculture (Gonçalves et al., 2008; Laclau et al., 2010). Large N removal at harvest is, up to now, mainly compensated by fertilization. However, the increasing cost of fertilizers and related environmental issues (water pollution and greenhouse gas emissions) favor the emergence of alternative management options to reduce fertilizer inputs taking better advantage of ecological mechanisms that occur in natural ecosystems to sustain productivity (Malezieux, 2012). A slight reduction in productivity could well be worth the reduced fertilizer costs if difficulties for implementing mixed-species plantations are overcome by forest managers.

Mixed-species forest plantations with a nitrogen-fixing species (NFS) are one of these options (Binkley, 1992; Forrester et al., 2006c; Kelty, 2006; Piotta, 2008). The introduced NFS is thought to provide N to the stand maintaining soil fertility that would stimulate growth of the non-fixing – target – species and wood production at the stand level (DeBell et al., 1997; Khanna, 1997b; Parrotta, 1999; Binkley et al., 2003; Bristow et al., 2006; Sayyad et al., 2006). However, mixed-species stands are sometimes less productive than target species in monoculture (Binkley et al., 1992; Petit and Montagnini, 2006; Laclau et al., 2008). The success of mixed-species plantations depends on species attributes and site factors (Forrester et al., 2005b) that affect the balance of positive and negative interactions between the species (Boyden et al., 2005). Two positive interactions may contribute to enhance stand productivity in mixed-species plantations with NFS (Fridley, 2001; Kelty, 2006). First, complementarity, which results of differences in resource requirements between the species in the mixture when the interspecific competition is lower than the intraspecific one, leads to a better use of available resources at the stand level. This may result from a higher light interception resulting from canopy stratification (Bauhus et al., 2004; Le Maire et al., 2012) that may enhance gross primary production but also water use (Forrester et al., 2010). Second, N fixation by NFS is supposed to improve soil N availability (Khanna, 1997a; Bouillet et al., 2008; Voigtlaender et al., 2012), alleviating N limitation and facilitating the growth of the target species in N limited soils (Forrester et al., 2005a, 2007). In addition, NFS may enhance phosphorus (P) availability through the rhizosphere acidification due to nitrogen fixation (Hinsinger et al., 2011), increasing the amount of P that cycles in mixed-species plantations compared to monocultures (Forrester et al., 2005a). However, these positive effects may, in some circumstances, be offset by an increase in competition for other limiting resources (Forrester et al., 2006a). The balance between competition, complementarity and facilitation affects resource capture, resource use and resource use efficiency (Fridley, 2001; Cardinale et al., 2007, 2011). These are key points for understanding the conditions that are required so that mixed-species plantations will outperform eucalypt monocultures in terms of wood production.

While canopy photosynthesis determines the overall carbon (C) acquisition by the stand, it is not directly related to stand production as only a part goes to the production of wood. Carbon allocation, defined here as the partitioning of NPP among the different compartments of the trees, varies with resource availability (Litton et al., 2007). Carbon allocation is predicted to be tuned to maintain an optimal internal resource status by acquiring a balanced supply of resources (Farrar and Gunn, 1998). As expected from this concept, the amount of C allocated to belowground production (BNPP) shifts toward aboveground production (ANPP), and especially wood production (wood NPP), with increasing soil fertility (Keith et al., 1997; Ryan et al., 2004; Litton et al., 2007; Campoe et al., 2012; Epron et al., 2012). Because the introduction of a NFS in a

eucalypt plantation is thought to increase the amount of available N in the soil (Voigtlaender et al., 2012), a higher fraction of carbon is thought to be allocated aboveground in the mixed-species stand than in the eucalypt monoculture. While such a shift was reported when comparing a monoculture of *Eucalyptus globulus* and a mixed-species stand with *Acacia mearnsii* in South East Australia (Forrester et al., 2006b), an opposite response was observed for a mixed-species stand of *Eucalyptus grandis* and *Acacia mangium* in South East Brazil (Nouvellon et al., 2012). The later response in terms of growth and carbon allocation was observed despite an effective N fixation by the acacia trees (Bouillet et al., 2008) and an improvement of the soil N status (Voigtlaender et al., 2012). Despite the scarcity of studies on C allocation in mixed-species plantations with NFS, the comparison of these two studies suggests that the response is site-specific.

In the present study, we aimed at comparing the influence of replacing half of eucalypt trees by *A. mangium* trees on C allocation in two contrasting tropical environments in Brazil and in Congo. While we already know that the mixed-species stand at the Brazilian site produced less wood than the eucalypt monoculture partly because of a lower partitioning to wood production (Nouvellon et al., 2012), we hypothesized that more C is allocated to ANPP and less to BNPP in the mixture than in the eucalypt monoculture at the Congolese site characterized by a soil of extremely low fertility (clay, C and N contents much lower than at the Brazilian site, Laclau et al., 2010). We used a C mass-balance approach to estimate NPP and its partitioning between belowground, foliage and wood production, coupling measurements of standing biomass estimated from successive inventories and allometric relations, aboveground litterfall, changes in forest floor carbon and soil CO₂ efflux.

2. Materials and methods

2.1. Study site and experimental design

A similar experimental design was set up at two sites in Brazil and in Congo (Table 1). The Brazilian site is located at the Itatinga experimental station on a deep Ferralsol developed on Cretaceous sandstone, Marília formation, Bauru group (Laclau et al., 2008). The Congolese site is located on a plateau close to Kissoko village on a deep Ferralic Arenosol laying on a geological bedrock composed of thick detritic layers of continental origin dated from plio-pleistocene (Mareschal et al., 2011). Climate is tropical at Itatinga and subequatorial at Kissoko with in both cases a cooler dry season extending from June to September. In Brazil, the previous land use was *Eucalyptus saligna* Sm. plantations set up on savannah (cerado) in 1940 and managed as an unfertilized coppice till 1998, followed by a *E. grandis* rotation with a low level of fertilization (300 kg ha⁻¹ of NPK 10:20:10). In Congo, the original vegetation was native tropical grassland dominated by the poaceae *Loudetia arundinacea* (Hochst.) Steud, that was afforested in 1984 with eucalypt hybrids with a starter fertilization (150 g of NPK 13:13:21 per tree). The stumps of the previous stand rotation were devitalized by glyphosate application at both sites and only debarked commercial-sized boles (top-end over-bark diameter exceeding 2 cm) were removed while harvest residues were spread uniformly.

A complete randomized block design was established in May 2003 with four blocks at Itatinga (stocking density, 1111 trees per ha) and in May 2004 with five blocks at Kissoko (800 trees per ha, Table 1). These densities reflect the current densities in commercial plantations and lead to the maximum stem wood production in eucalypt monocultures at both sites. Each plot consisted in an inner part of 36 trees (6 × 6) and two buffer rows, and were

Table 1
Main characteristics of the two experimental sites.

	Itatinga (Brazil)	Kissoko (Congo)
Latitude	23°02'S	4°44'S
Longitude	48°38'W	12°01'E
Elevation (m)	860	100
Annual precipitation (mm)	1370 [1320] ^a	1430 [1660] ^b
Averaged daily mean temperature (°C)	19.0 ^a	25.7 ^b
Soil (WRB classification)	Ferralsols	Ferralic arenosols
Clay:silt:sand (%) ^c	13:3:84	3:6:91
C (g kg ⁻¹)	17.6	6.9
N (g kg ⁻¹)	0.9	0.4
Species	<i>E. grandis</i> (seeds from Suzano Co)	<i>E. urophylla</i> x <i>grandis</i> (clone 18–52)
	<i>A. mangium</i>	<i>A. mangium</i>
	Collected in Amazonia ^d	Collected in Congo ^d
Tree density (tree ha ⁻¹)	1111	800
Fertilization (kg ha ⁻¹)	Dolomite limestone ^e (2000), P ^f (44, superphosphate), K ^f (10, potassium chloride), Fe ^f (7), B ^f (3), Zn ^f (3), Mn ^f (1), K ^g (75),	N ^e (43, ammonitrate)
Age at harvest (years)	6	7

^a Average from January 2003 to December 2009 (during the measurement period under bracket). Data provided by the Itatinga experimental station.

^b Average from January 2004 to December 2011 (during the measurement period under bracket). Data provided by Pointe-Noire airport located 30 km from the experimental site.

^c Soil mineralogy is for the 0–50 cm soil layer and soil chemistry is for the 0–5 cm soil layer. Data from Voigtlaender et al. (2012) for Itatinga and from Nouvellon et al. (2008) for Kissoko (except N that is unpublished).

^d Seeds from best provenances grown in trials in Amazonia and in Congo, but information about the selected lines is not available.

^e Applied at planting (SiO₂ 11.92%, Al₂O₃ 1.01%, Fe₂O₃ 0.54%, MnO 0.13%, MgO 18.33%, CaO 25.61%, Na₂O 0.15%, K₂O 0.16%, TiO₂ 0.05%, P₂O₅ 0.06%, Loss on ignition [110–1000 °C] 40.81%).

^f Dug in holes at 20 cm from the plants.

^g Applied in three times 6, 12 and 18 months after planting.

either monoculture plots of acacia (100A), monoculture plots of eucalypt (100E) or mixed-species plots in a proportion of 1:1 of both species (50A:50E, the two species being alternately planted in the row, and between adjacent rows). Except for nitrogen, fertilizers were applied according to the commercial silviculture at both sites (Table 1). Our study was carried out in 3 of the four blocks at Itatinga and in 2 of the five blocks at Kissoko. Destructive sampling for biomass measurements were done on the other blocks. A complete description of the experimental layout is given in Bouillet et al. (2012). The experiments were conducted at the end of the rotation prior harvesting that typically occurred when the trees are 6 year-old in the state of São Paulo (Itatinga) in Brazil and 7 year-old in the Kouilou region (Kissoko) in Congo, based on forestry knowledge accumulated on both sites (production curves).

2.2. Tree census and biomass measurements

Tree height (H , m) and circumference at 1.3 m height (C_{130} , cm) were measured at least once a year on 36 trees per plot (excluding the buffer rows). The diameter (D , m) of each tree was computed from C_{130} . Most of the acacias were multi-stem trees and the circumference of all the stems exceeding 2 cm in diameter at 1.3 m height was measured, the cross sectional area of all the stems was cumulated for each tree and an “equivalent diameter” was calculated from the total cross sectional area of the tree.

Aboveground biomass, i.e. stem wood, stem bark, living branches, dead branches and leaves, were measured by sampling 10 trees of each species in each treatment 4 and 6 years after planting. Trees were selected to account for the distribution of cross-section areas in each treatment (monoculture and mixed-species plantations). Coarse root biomass (diameter above 2 mm, B_R) was measured on a subsample of trees at 72 months (15 and six trees per species at Itatinga and Kissoko respectively) as described with more details in Nouvellon et al. (2012).

The fresh mass of all tree compartments was measured in the field and subsamples were brought back to the laboratory,

oven-dried at 65 °C and weighed. Allometric relationships were established for each compartment:

$$B_X = \alpha_X + \beta_X \times (D^2 \times H)^{\gamma_X} \quad (1)$$

with B (kg), the biomass, D (m), the diameter computed from C , and α , β and γ the allometric coefficients to be estimated for the compartment X . The equations were fitted by species and treatment using PROC NLP in the SAS 9.2 software (SAS Institute Inc., Cary, NC, USA) and, for a given species, the Akaike information criterion was used to decide whether a different set of allometric coefficients should be used for each of the two treatments or whether a single set could be used for both treatments. The selected allometric relationships were then applied to the plot inventories and dry matter were converted in biomass carbon (C_X , kg m⁻² of C) using the carbon content of each component.

Live fine roots were sorted from nine cores per plot at Itatinga and five cores per plot at Kissoko collected with a root auger (internal diameter of 8 cm) down to a depth of 1 m. Roots sampled in monospecific stands were used to facilitate the identification of each species for roots collected in the mixed-species plots.

Leaf area index (LAI) was obtained for each species and treatment from allometric relationships relating leaf area of harvested trees to D . Tree leaf area was estimated for each sampled tree from measurements of the leaf biomass and specific leaf area (SLA) in three crown sections (lower, middle, upper) as described in Nouvellon et al. (2010). Because LAI is dynamic over the course of a year and the relation between D and leaf area changes with stand age, the estimation of LAI is thus only valid at the age of the destructive sampling.

2.3. Soil CO₂ efflux and total belowground carbon flux

Soil CO₂ efflux (μmol m⁻² s⁻¹) was measured every two weeks during the two last years of the rotation at Itatinga (from 48 to 72 months after planting) and during the last year of the rotation at Kissoko (from 78 to 90 months after planting) with a dynamic closed-path Li8100 system equipped with a 20 cm diameter

Li8100-103 soil CO₂ efflux chamber (LiCor Inc., Lincoln, NE, USA). The stability of the infrared gas analysers was checked at regular intervals and they were calibrated when needed. Nine PVC collars were installed in each monoculture plot about 1 month before the beginning of the measurements. The number of collars per plot was increased to 18 at Itatinga and 13 at Kissoko in the mixed-species plots. Soil volumetric water content in the 0–6 cm soil layer (SWC, m³ m⁻³) and within 5 cm from the collars was measured at the same time with a soil moisture probe (Theta Probe ML2X, Delta-T Device Ltd., Cambridge, UK). Annual soil CO₂ efflux (kg m⁻² year⁻¹ of C) was estimated for each PVC collar using linear interpolations of soil CO₂ efflux between each measurement date over the period of measurement covering two (Itatinga) or one (Kissoko) full year.

Aboveground litterfall was collected every month in 51 traps (52 cm × 52 cm) at Itatinga and in four traps (75 cm × 75 cm) at Kissoko in each monoculture plot. The number of traps was increased to 10 at Itatinga and 6 at Kissoko in the mixed-species plots. Litter was separated by species and components, oven-dried at 65 °C and weighed. Branches were collected over a 3 m × 3 m area in each plot. Annual litterfall (kg m⁻² year⁻¹ of C) was obtained by summing monthly litterfall measurements, multiplied by C concentrations of the different litter compartments.

Litter on the forest floor was collected at ages of 48 and 72 months at Itatinga with a 15-cm radius circular frame and at ages of 78 and 90 months at Kissoko with a square metallic frame (50 cm × 50 cm) in each plot and sorted into leaves, twigs, bark, and miscellaneous, oven-dried at 65 °C and weighed. Nine (monoculture) to 18 (mixed-species plantation) samples were collected in each plot at Itatinga and 4–6 at Kissoko. Ash content was determined after combustion of pooled samples in a muffle furnace at 450 °C for 6 h, and used to correct the dry mass for soil contamination. The forest floor carbon (C_L, kg m⁻² of C) was computed from the dry weight and C concentrations of the different forest floor components.

Total belowground carbon flux (TBCF, kg m⁻² year⁻¹ of C) was estimated using a mass balance approach (Giardina and Ryan, 2002; Epron et al., 2012):

$$TBCF = F_{CUM} + \Delta C_R - L_{CUM} + \Delta C_L + \Delta C_S + E \quad (2)$$

where ΔC_R is the annual increment of root biomass carbon, ΔC_L is the annual build-up of forest floor carbon, ΔC_S is the annual increase in the carbon content of the mineral soil and E is the flux of the C transported off the site by leaching of the dissolved organic and inorganic C, by erosion or by CH₄ emission. We assumed a constant fine root (diameter < 2 mm) biomass and necromass at this age, no change in soil organic matter over the short measurement period and no exportation of soil carbon off-site (Epron et al., 2012). We also neglected the decomposition of stumps and coarse root from the previous rotation since accounting for that only marginally decrease the TBCF estimated at the end of the rotation at Itatinga (Nouvellon et al., 2012).

2.4. Aboveground and belowground net primary production

Annual net production of foliage (foliage NPP, kg m⁻² year⁻¹ of C) was estimated as the yearly difference in standing biomass carbon of leaves plus the amount of leaf carbon recovered in the annual aboveground litterfall. Annual net production of wood (wood NPP, kg m⁻² year⁻¹ of C) was estimated as the yearly difference in standing biomass carbon of stem wood, stem bark and branches plus the amount of stem bark and dead branch carbon recovered in the annual aboveground litterfall. Aboveground net primary production (ANPP, kg m⁻² year⁻¹ of C) was calculated as the sum of foliage NPP and wood NPP.

Belowground net primary production (BNPP, kg m⁻² year⁻¹ of C) was calculated assuming that belowground autotrophic respiration is a constant fraction of BNPP:

$$BNPP = TBCF \times CUE \quad (3)$$

where CUE is the carbon-use efficiency of belowground production. We assumed CUE for belowground production of 0.5 (Binkley and Ryan, 1998; Litton and Giardina, 2008; Nouvellon et al., 2012).

Table 2

Leaf area index (LAI), leaf and woody carbon biomasses (B_L and B_W) and production (foliage NPP and wood NPP), aboveground litterfall, fine root and coarse root carbon biomass (B_{FR} and B_R), yearly increment in coarse root carbon biomass and forest floor carbon (ΔB_R and ΔC_L), annual soil CO₂ efflux (F_S), total belowground carbon flux (TBCF), aboveground, belowground and total net primary production (ANPP, BNPP and NPP), BNPP to NPP ratio and wood NPP/NPP ratio for acacia and eucalypt monocultures (A100 and E100) and for mixed-species plots (50A:50E) at the end of the rotation (6 years at Itatinga, 7 years at Kissoko). Annual fluxes and productions are for the two last years of the rotation at Itatinga, for the last year at Kissoko. Mean and standard deviations are given for 2 (Kissoko) or 3 (Itatinga) replicates (blocks). Annual F_S was calculated from nine collars per block in monocultures and 13 (Kissoko) or 18 (Itatinga) collars per block in mixed-species plots. P values for the effects of site (S, Itatinga and Kissoko), treatment (T, 100A, 100E and 50A:50E) and their interaction are given. Mean values followed by different letters are significantly different at $P = 0.05$ within a site. For a given treatment, values followed by an asterisk are significantly different at $P = 0.05$ between the two sites.

	Statistics (P values)			Itatinga (Brazil)			Kissoko (Congo)		
	S	T	S*T	100A	100E	50A:50E	100A	100E	50A:50E
LAI (m ² m ⁻²)	0.001	0.002	ns	4.29 ± 0.50b	3.84 ± 0.14a	5.44 ^a ± 0.26b	3.51 ± 0.04ab	2.97 ± 0.38a	3.95 ^b ± 0.64b*
B_L (kg m ⁻²)	<0.001	0.002	ns	0.26 ± 0.04a	0.25 ± 0.02a	0.33 ± 0.03b	0.24 ± 0.01b	0.14 ± 0.01a*	0.24 ± 0.03b*
Foliage NPP (kg m ⁻² year ⁻¹)	0.004	<0.001	0.013	0.28 ± 0.02c	0.19 ± 0.01a	0.23 ± 0.02b	0.27 ± 0.01a	0.24 ± 0.02a*	0.28 ± 0.00a*
B_W (kg m ⁻²)	0.001	0.010	0.009	4.61 ± 0.55a	6.14 ± 0.22b	5.29 ± 0.35a	3.86 ± 0.21a	3.80 ± 0.61a*	4.98 ± 0.39b
Wood NPP (kg m ⁻² year ⁻¹)	0.001	0.014	0.013	1.00 ± 0.18a	1.44 ± 0.07b	1.04 ± 0.12a	0.59 ± 0.00a*	0.73 ± 0.15ab*	1.00 ± 0.19b
ANPP (kg m ⁻² year ⁻¹)	0.001	0.043	0.013	1.28 ± 0.19a	1.62 ± 0.07b	1.27 ± 0.13a	0.86 ± 0.01a*	0.97 ± 0.12ab*	1.29 ± 0.19b
Litterfall (kg m ⁻² year ⁻¹)	0.002	0.015	0.007	0.30 ± 0.01a	0.43 ± 0.03b	0.40 ± 0.04b	0.32 ± 0.02a	0.29 ± 0.04a*	0.32 ± 0.01a*
B_{FR} (kg m ⁻²)	ns	ns	0.013	0.11 ± 0.01a	0.09 ± 0.02a	0.12 ± 0.00a	0.09 ± 0.00ab	0.13 ± 0.05b	0.06 ± 0.00a*
B_R (kg m ⁻²)	ns	<0.001	ns	0.71 ± 0.08a	1.29 ± 0.04b	1.18 ± 0.09b	0.69 ± 0.03a	1.09 ± 0.19b	1.16 ± 0.13b
ΔB_R (kg m ⁻² year ⁻¹)	0.003	0.009	ns	0.16 ± 0.03a	0.24 ± 0.02b	0.21 ± 0.02ab	0.09 ± 0.00a*	0.17 ± 0.04b*	0.16 ± 0.05ab
ΔC_L (kg m ⁻² year ⁻¹)	<0.001	0.010	0.009	-0.03 ± 0.06a	0.18 ± 0.03b	0.15 ± 0.02b	-0.08 ± 0.04a	-0.10 ± 0.05b*	-0.11 ± 0.11b*
F_S (kg m ⁻² year ⁻¹)	<0.001	0.043	ns	0.99 ± 0.05a	1.13 ± 0.09b	1.20 ± 0.08b	1.38 ± 0.07a*	2.02 ± 0.30b*	1.78 ± 0.41b*
TBCF (kg m ⁻² year ⁻¹)	0.009	0.025	ns	0.82 ± 0.10a	1.13 ± 0.13a	1.16 ± 0.08a	1.07 ± 0.04a	1.80 ± 0.43b*	1.51 ± 0.45ab
BNPP (kg m ⁻² year ⁻¹)	0.009	0.025	ns	0.41 ± 0.05a	0.56 ± 0.07a	0.58 ± 0.04a	0.54 ± 0.02a	0.90 ± 0.21b*	0.75 ± 0.23ab
NPP (kg m ⁻² year ⁻¹)	ns	0.006	ns	1.69 ± 0.22a	2.19 ± 0.13b	1.85 ± 0.16ab	1.39 ± 0.01a	1.87 ± 0.34b	2.04 ± 0.03b
BNPP/NPP (%)	<0.001	ns	0.038	24 ± 2a	26 ± 2a	31 ± 2a	38 ± 1a*	48 ± 3b*	37 ± 11a
Wood NPP/NPP (%)	<0.001	ns	0.015	59 ± 3a	66 ± 1b	56 ± 2a	42 ± 0ab*	39 ± 1a*	49 ± 10b

^a 41% From acacia (2.23) and 59% from eucalypt (3.20).

^b 40% From acacia (1.56) and 60% from eucalypt (2.39).

2.5. Statistical analyses

Statistical analyses were performed with R software version 2.13.0 (R Development Core Team, 2011). Mixed-effect models with blocks as a random effect were used to estimate the effects of site (Itatinga and Kissoko) and treatment (100A, 100E and 50A:50E) on all variables showed in Table 2 and the effect of site, species and plantation mode (monoculture or mixed-species) on tree dimension (D^2H and H/D^2). Contrasts were used to test relevant differences between treatments within a site and between sites for each treatment.

3. Results

3.1. Tree dimensions, stand biomass and leaf area index

At individual tree level, the growth of acacias was markedly reduced in the mixed-species plantation compared to acacia monoculture at Itatinga while there was no difference at Kissoko. The volume index of individual trees at harvest (D^2H) was 54% lower for acacia in the mixed-species plots compared to the monoculture at Itatinga. In contrast to acacia, the growth of eucalypts was enhanced in the mixed-species plots compared to the monoculture at both sites, but the stimulation was greater at Kissoko than at Itatinga. D^2H of eucalypt at harvest were enhanced by 46 and 103% in mixed-species plots at Itatinga and Kissoko respectively (Fig. 1A and B). In the mixed-species plots, eucalypt trees were significantly taller than acacia trees at both sites at harvest (25.3 m compared to 12.8 m at Itatinga and 28.5 m compared to 19.5 m at Kissoko, data not shown) leading to a stratified canopy. The height-to-diameter square ratio of individual trees (H/D^2) was lower in the mixed-species plots than in the monoculture for eucalypt at both sites. Acacia in the mixed-species plots did not exhibit significant difference in H/D^2 compared to the monoculture (Fig. 1C and D).

Stand level wood (B_W) and leaf (B_L) carbon biomasses were significantly higher at Itatinga than at Kissoko for eucalypt monoculture, while the differences were not significant for acacia plots. B_W was significantly higher in the mixed-species plots than in eucalypt monoculture at Kissoko while the opposite was observed at Itatinga (Table 2). LAI was higher at Itatinga than at Kissoko in mixed-species plots, while the differences were not significant for the two monocultures (Table 2). At both sites, LAI (and B_L) in the mixed-species plots were significantly higher than in eucalypt monocultures. Eucalypt trees had a strong contribution to stand LAI in the mixed-species plots at both sites. Eucalypt LAI in the mixed-species plots was maintained at about 80% of the LAI in the monoculture despite a twofold lower stocking density, while the LAI of acacia trees was only 52% (Itatinga) and 44% (Kissoko) of that in the monoculture. Coarse and fine root carbon biomass did not differ significantly between the two sites, except for B_{FR} in the mixed-species plots that was much lower at Kissoko than at Itatinga, due to an opposite trend at the two sites. While B_{FR} was significantly lower in the mixed-species plots than in eucalypt monoculture at Kissoko, the difference was not significant at Itatinga (Table 2).

3.2. Aboveground litterfall, soil CO_2 efflux and total belowground carbon flux

Annual aboveground litterfall was significantly higher at Itatinga compared to Kissoko, except for the acacia. Annual litterfall was significantly lower in the acacia monoculture than in the two other types of plots at Itatinga (Table 2). This was mainly due to a much lower contribution of woody litterfall in acacia monoculture (8%) than in the eucalypt monoculture (49%) and in the mixed-species plots (39%). The contribution of woody litter to annual litterfall was similar in all plots at Kissoko (25–28%).

Soil CO_2 efflux exhibited seasonal fluctuations that paralleled the seasonal fluctuation in soil water content (Fig. 2A and B) with

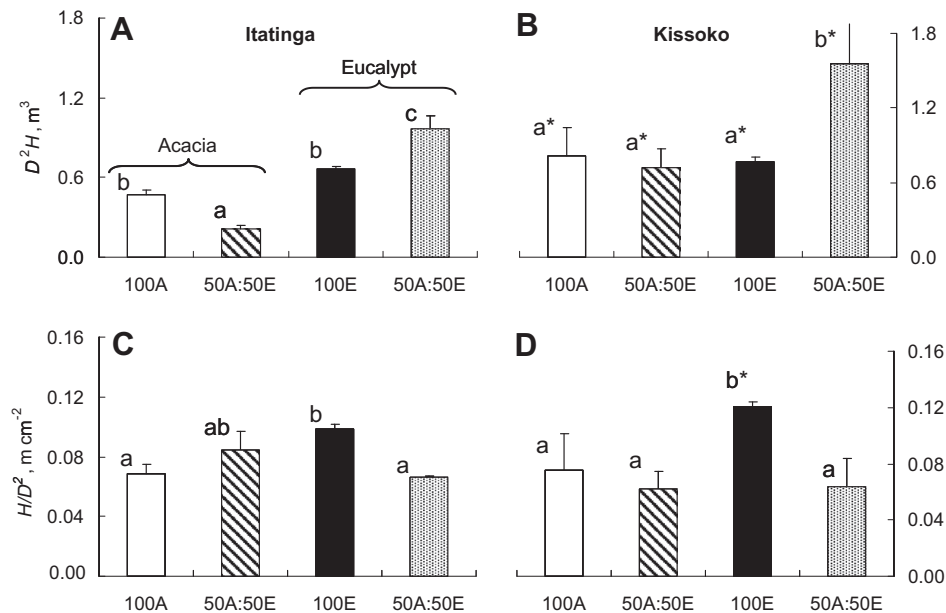


Fig. 1. Tree volume index (D^2H with D , diameter at 1.3 m high and H , tree height, upper panels, A and B) and height to square diameter ratio (H/D^2 , lower panels, C and D) for acacias in monoculture (open bars), acacias in the mixed-species plots (hatched bars), eucalypts in monoculture (closed bars) and eucalypts in mixed-species stands (dotted bars) at the end of the rotation at Itatinga (6 year-old, left, A and C) and Kissoko (7 year-old, right, B and D). Stand densities were 1111 trees per ha at Itatinga and 800 trees per ha at Kissoko. Mean and standard deviations of 36 trees per plot (monoculture plots) or 18 trees per plot and per species (mixed-species plots) for 2 (Kissoko) or 3 (Itatinga) plots (blocks) are given. Different letters indicate significant differences at $P = 0.05$ within a site. Asterisks indicate significant differences at $P = 0.05$ between the two sites for a given treatment.

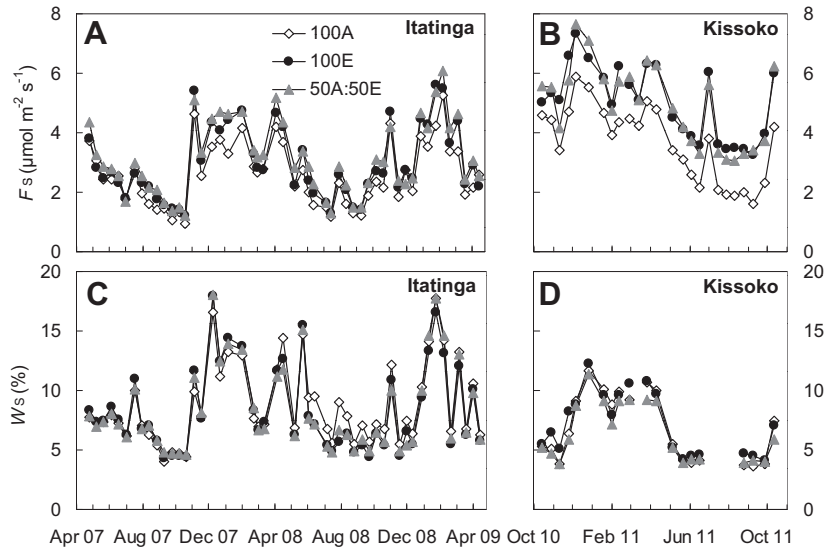


Fig. 2. Soil CO₂ efflux (F_s , upper panels, A and B) and soil water content (W_s , lower panels, C and D) measured every 2 weeks for 2 years at Itatinga (4–6 year-old, left, A and C) and for 1 year at Kissoko (6–7 year-old, right, B and D). Mean of nine collars per monoculture plot and 13 (Kissoko) or 18 (Itatinga) collars per mixed-species plots for 2 (Kissoko) or 3 (Itatinga) plots (blocks) are given. Standard deviations are not shown for clarity but refer to Table 2 for statistics on cumulative annual soil CO₂ efflux.

greater values during the wet/warm season than during the dry/cold season at both sites. The peak of soil CO₂ efflux that occurred in July at Kissoko during the dry season was explained by a small rainfall event that occurred during the night prior the measurement (3.0 mm recorded by a nearby weather station, data not shown). Cumulative soil CO₂ efflux was significantly lower in the acacia monoculture than in the two other treatments at both sites and, overall, annual F_s was significantly lower at Itatinga compared to Kissoko whatever the treatment (Table 2).

The amount of carbon on the forest floor slightly decrease during 1 year at Kissoko in all plots but increased markedly over the two measurement years at Itatinga for the eucalypt monoculture and the mixed-species plots leading to an annual build-up of forest floor carbon (ΔC_f) of about one-third of annual litterfall (Table 2).

Differences in total belowground carbon flux were not significant among treatment at Itatinga (Table 2). Higher annual F_s and higher root biomass increment in eucalypt plots than in acacia plots were offset by a higher annual litterfall. This was not observed at Kissoko where TBCF was higher for eucalypt than for acacia plots. TBCF was higher at Kissoko than at Itatinga for the eucalypt plots and the mixed-species plots because of a higher annual F_s and lower annual litterfall that were not compensated by a slightly lower root biomass increments.

3.3. Net primary production

Because belowground net primary production was calculated as a fixed fraction of TBCF, differences in BNPP between the two sites and among the treatments were the same as differences in TBCF (higher BNPP for eucalypt than for acacia plots at Kissoko and higher BNPP at Kissoko than at Itatinga for the eucalypt plots, Table 2). The higher BNPP at Kissoko compared to Itatinga was not explained by the difference in annual increments of coarse root biomass.

In contrast to BNPP, ANPP was higher at Itatinga than at Kissoko for both acacia and eucalypt monoculture plots while no difference was observed between the mixed-species plots of both sites because ANPP was lower in the mixed-species plots than in the eucalypt plots at Itatinga, due to a much lower wood production (wood NPP) that was not compensated by the higher leaf production (foliage NPP, Table 2).

Net primary production was not significantly different between Itatinga and Kissoko and differences in ANPP and wood NPP between the two sites were related to change in the partitioning of NPP (i.e. the relative contribution of ANPP and BNPP to NPP), not to change in NPP (Table 2). The BNPP to NPP ratios were 38% for acacia and 48% for eucalypt at Kissoko, values almost twice as high

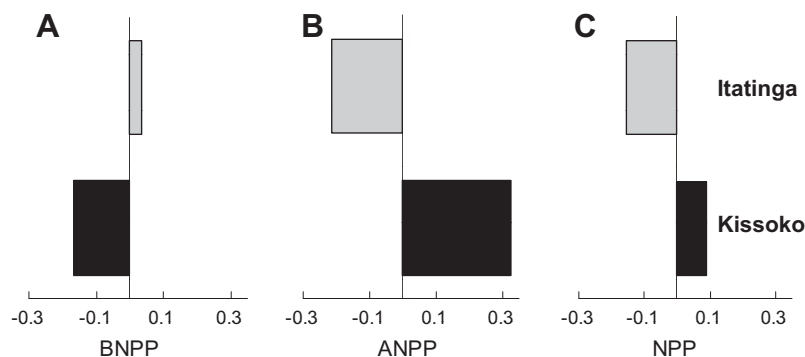


Fig. 3. Belowground net primary production (BNPP, A), aboveground net primary production (ANPP, B) and net primary production (NPP, C) in mixed-species plots expressed relative to eucalypt monoculture (50A:50E/100E-1) at Itatinga (open bars) and Kissoko (closed bars). Productions are for the two last years of the rotation at Itatinga (4–6 year-old) and for the last year at Kissoko (6–7 year-old).

as those observed at Itatinga (24% and 26% respectively). At Itatinga, there was no marked difference in NPP between the acacia monoculture and the mixed-species plots. NPP of eucalypt monoculture was higher than NPP of mixed-species plots. At Kissoko, the eucalypt monoculture and the mixed-species plots exhibited higher NPP than the acacia monoculture. NPP of the mixed-species plots at Kissoko was significantly higher than the average NPP of the two monocultures (2.04 ± 0.03 versus 1.63 ± 0.16).

At Itatinga, the partitioning of NPP to belowground was higher in the mixed-species plots (31%) compared to the monocultures, while it was lower at Kissoko (37% in the mixture versus 48% in E100). These opposite shifts in NPP partitioning between the two sites (Fig. 3) explained why wood NPP was significantly lower in the mixed-species plots compared to the eucalypt monoculture at Itatinga and slightly higher at Kissoko. While wood NPP contributed to NPP much more at Itatinga than at Kissoko in the eucalypt monocultures (66% and 39% respectively) and in the acacia monocultures (58% and 42%), the difference between the two sites almost vanished in the mixed-species plots (Table 2).

4. Discussion

The two experimental sites differed by soil and climate characteristics, and by silvicultural practices such as stocking density, fertilization, rotation length and genetic materials that mimicked the practices in commercial plantations at both sites. While NPP did not differ significantly between these two contrasting case studies, its partitioning between above and belowground growth were significantly different, as was the effect of interplanting acacia on carbon allocation, eucalypt growth and stand level wood production.

4.1. NPP partitioning in eucalypt stands differs between the two sites

The maximal commercial productivity of eucalypt stands with the best *Eucalyptus urophylla* × *grandis* clones used for afforestation in the Kouilou region reaches a ceiling of $30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (P. Vigneron, CRDPI breeding program, personal communication) while a productivity above $40 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ is commonly reached in Brazil (Gonçalves et al., 2008; Marsden et al., 2010). Wood production at Itatinga at the end of the rotation was indeed twice as high as that at Kissoko, a difference that fully account for the observed difference in ANPP because leaf production was similar at both sites (0.19 and $0.24 \text{ kg m}^{-2} \text{ year}^{-1}$ of C). ANPP at Itatinga ($1.62 \text{ kg m}^{-2} \text{ year}^{-1}$ of C) was similar to that reported for a nearby 6-year-old stand of *E. grandis* (Epron et al., 2012). Cumulative soil CO_2 efflux was higher at Kissoko than at Itatinga. Because annual F_5 is the largest component of TBCF (Giardina and Ryan, 2002), an additional year of measurement would have been needed to get a more accurate mass balance at Kissoko. The total belowground carbon flux (1.13 and $1.80 \text{ kg m}^{-2} \text{ year}^{-1}$ of C at Itatinga and Kissoko), from which BNPP is derived, was lower at Itatinga than at Kissoko, and in the range of values reported for tropical eucalypt plantations (0.4 – 2.6 , Giardina et al., 2003; Stape et al., 2008; Ryan et al., 2010; Campoe et al., 2012; Epron et al., 2012; Nouvellon et al., 2012). Direct estimates of CUE for belowground production are lacking, severely constraining our ability to derive accurately BNPP from TBCF (Litton and Giardina, 2008). Assuming a constant CUE belowground, the lower ANPP at Kissoko compared to Itatinga was almost fully balanced by a higher BNPP, leading to a small, non-significant difference in total NPP at both sites (2.19 and $1.87 \text{ kg m}^{-2} \text{ year}^{-1}$ of C at Itatinga and Kissoko, respectively).

Fertilization is known to increase partitioning to ANPP at the expense of BNPP in forest ecosystems (Litton et al., 2007) and especially in eucalypt plantations (Keith et al., 1997; Giardina et al., 2003; Epron et al., 2012). The total nitrogen stock in the 0–50 cm

soil layer at a site nearby Kissoko is only about 20% of that at Itatinga but the Congolese soil contains more phosphorus than that of Itatinga (Laclau et al., 2010). As a consequence, previous studies have shown that stem biomass of eucalypt trees at the end of the rotation was enhanced by nitrogen fertilization only the first 2 years after planting at Itatinga (Laclau et al., 2009) whereas it was largely increased throughout the rotation at Kissoko (Bouillet et al., 2004).

Differences in nitrogen availability between Itatinga and Kissoko might partly account for the difference in partitioning between above- and belowground productions between the two sites. Water deficit is also known to affect NPP partitioning in eucalypt plantations (Stape et al., 2008; Ryan et al., 2010). We cannot therefore rule out a confounding influence of water limitation on the difference in NPP partitioning between the two sites owing to the difference in soil texture, leading to lower water holding capacity at Kissoko than at Itatinga, and to the longer dry season at Kissoko compared to Itatinga. However, differences in silvicultural practices (stocking density, fertilization regime) and in genetics materials between the two sites preclude any firm conclusions about factors that drive the difference in C partitioning between the two sites.

The difference in TBCF between the two sites was related to a higher annual F_5 and a lower annual litterfall at Kissoko than at Itatinga, suggesting that differences in annual F_5 between the two sites are more likely explained by differences in autotrophic respiration (R_A), including root and associated microorganisms (Hanson et al., 2000; Epron, 2009). Fine roots have high specific respiration rates and contribute to a large proportion of total root respiration at stand level (Marsden et al., 2008a,b; Thongo M'Bou et al., 2010). Autotrophic sources accounted for 60% of annual F_5 in a 9-year old Congolese eucalypt plantation at a nearby site (Epron et al., 2006). The contribution of autotrophic sources to soil CO_2 efflux was not estimated in this study but because we assumed a CUE of 0.5 to estimate BNPP, R_A is thus equal to BNPP, and thus lower at Itatinga than at Kissoko. The higher TBCF at Kissoko compared to Itatinga despite a lower coarse root biomass increment is likely related to a higher investment into fine root and/or mycorrhiza production and respiration, foraging for more limited nitrogen (Nadelhoffer et al., 1985; Tateno and Takeda, 2010).

4.2. Acacia stands have a lower productivity than eucalypt stands but exhibit similar site differences in partitioning

ANPP in acacia stands was higher at Itatinga than at Kissoko. But in contrast to eucalypt, the difference in ANPP was not fully offset by a higher BNPP. Average ANPP reported over a 7-year rotation for a nearby Congolese site (Bernhard-Reversat et al., 1993) was higher than those we measured at Kissoko (1.25 versus $0.86 \text{ kg m}^{-2} \text{ year}^{-1}$ of C) which may be explained by the fact that growth of *A. mangium* is maximal at age 4 years and decreases thereafter (Dupuy and N'Guessan, 1990).

Nitrogen fixation in acacia stands was not estimated at the end of the rotation but was very different between the two sites at age 2.5 years based on ^{15}N natural abundance (Bouillet et al., 2010). Much higher values were estimated at Kissoko (nitrogen-limited site, $21 \text{ g m}^{-2} \text{ year}^{-1}$ of N) than at Itatinga ($2.6 \text{ g m}^{-2} \text{ year}^{-1}$). Nitrogen fixation at Kissoko was almost twice the average values reported for *A. mangium* plantations in the Philippines (Mercado et al., 2011). The carbon cost of symbiotic nitrogen fixation is thus higher at Kissoko compared to Itatinga. Assuming that 5 g of C is required to fix 1 g of N (Cannell and Thornley, 2000), the extra cost of nitrogen fixation will be $105 \text{ g m}^{-2} \text{ year}^{-1}$ of C at Kissoko and $13 \text{ g m}^{-2} \text{ year}^{-1}$ at Itatinga, respectively 10% and 1% of TBCF, thus not accounting for difference in TBCF between acacia and eucalypt stands. TBCF was even significantly lower in the acacia than in the

eucalypt stands at Kissoko, which contrasts with previous results showing a lower TBCF in eucalypt plantations compared to nearby acacia (Forrester et al., 2006b) and albizia (Binkley and Ryan, 1998) plantations.

As for eucalypt stands, the high TBCF at Kissoko in comparison with Itatinga was not explained by a higher increment of coarse root biomass, thus indicating a higher fine root production and autotrophic respiration. TBCF was significantly higher for eucalypt than for acacia at Kissoko. The lower wood production and ANPP in acacia stands compared to eucalypt stands were not related to a preferential partitioning of NPP to belowground in acacia but to a lower NPP in acacia compared to eucalypt stands that was observed at both sites. These results contrast with those obtained on *E. saligna* and *Albizia falcataria* for which NPP was similar, while its partitioning was in favor of wood production in eucalypt stands (Binkley and Ryan, 1998). The cost of nitrogen fixation was not accounted for in our estimation of BNPP (we used the same CUE efficiency for belowground growth of eucalypts and acacias) but, based on the estimations given above, BNPP and NPP at Kissoko would have been overestimated by 14% and 5% respectively, and the BNPP to NPP ratio would have been 36% instead of 38%.

4.3. The effects of mixing acacia with eucalypt on net primary production and its partitioning is site-dependent

Replacing half of the eucalypts by acacia led to opposite results at Itatinga and Kissoko at the end of the first rotation, illustrating that site characteristics are key drivers of the success or failure of mixed-species plantations (Binkley, 1992; Forrester et al., 2005b). NPP was not significantly different in the mixture than in E100 despite opposite trends at the two sites. We did not observe any transgressive over-yielding for NPP as reported for mixtures of *E. globulus* and *A. mearnsii* in Southeast Australia (Forrester et al., 2006b). At Kissoko, despite no significant difference in NPP at the stand level (+9%), ANPP in the mixed-species stand was 33% higher than in E100, more than counterbalancing a 17% lower BNPP (Fig. 3). Wood biomass at harvest was significantly higher in the mixed-species plots than in the eucalypt monoculture at Kissoko (+31%). In contrast, ANPP was significantly lower (–22%) in the mixed-species stand at Itatinga, while BNPP remained almost unchanged (+4%, Fig. 3), leading to a significantly lower wood biomass at harvest (–14%) at the end of the first rotation. Long term monitoring is needed because the response may vary over time due to changes that may occur in soil fertility after several rotations.

Eucalypt trees were bigger at both sites in the mixed-species stands (D^2H , Fig. 1) but D^2H of acacia trees was depressed in the mixed-species stands compared to acacia monoculture at Itatinga, while it was not at Kissoko. A similar behavior was found in a pot trial, with *E. globulus* trees dominating and suppressing *A. mearnsii* trees at high level of N fertilizer (Forrester et al., 2006a). In our study, not only the size but also the form of eucalypt trees was affected by the presence of acacia, with a lower H/D^2 ratio in the mixed-species stands compared to the pure eucalypt stands at both sites. Our results contrast with those obtained on *E. globulus/A. mearnsii* mixture in which H/D ratios of eucalypt trees were similar to the eucalypt monoculture (Bauhus et al., 2000), and on *E. nitens/A. dealbata* mixture in which H/D ratios of eucalypt trees were higher than in the monospecific stand (Hunt et al., 2006). In this later study, increases in H/D ratios were explained by a preferential allocation of photosynthate to height growth in order to maintain a dominant canopy position. Because a vertical stratification was observed in our mixed-species stands at both sites, we hypothesize that competition for light was reduced for eucalypt trees. The difference in total LAI and LAI of the dominant species (eucalypts) between the two sites suggests that light might limit

more acacia growth in the mixed-species plantation at Itatinga than at Kissoko (Le Maire et al., 2012).

Higher LAI in mixed-species plantations compared to monocultures has also been found in southeast Australia in *E. globulus* and *A. mearnsii* mixed stands and it was related to a higher use of water by the mixed-species stand than by the monoculture (Forrester et al., 2010). Deep drainage amounted to 400–500 mm per year under eucalypt plantations at our study site in Congo (Laclau et al., 2005) while it was negligible at Itatinga from 2 years after planting onwards (Christina et al., 2011). Eddy covariance estimations of stand level transpiration have indeed shown that nearby eucalypt stands were using almost all the annual rainfall at Itatinga while they used only the two third of annual rainfall at Kissoko (Nouvelon et al., 2011). At Itatinga, the higher LAI in the mixed-species stands compared to the eucalypt monocultures might therefore speed up the depletion of available soil water at the beginning of the rotation, and then each year during the dry season, to the detriment of acacias. The low growth of acacia in the mixtures with eucalypts at Itatinga may indicate that *A. mangium* is at the limit of its climatic range at this site. Genetic improvement of *A. mangium* or the use of better adapted nitrogen fixing tree species may increase resource use efficiency alleviating the negative impact of competition on stand level productivity. Mixed-species plantations may also extract more water than monocultures at Kissoko, leading to less water loss by deep drainage and to a better use of available water at the stand level.

5. Conclusions

Replacing half of eucalypt trees by *A. mangium* trees has an opposite effect in two contrasted tropical sites. Mixed-species stand in the Brazilian site exhibited a lower stand wood increment and ANPP without change in TBCF. In contrast, the mixed-species stand over-yields the monocultures at the Congolese site, leading to a significantly higher standing wood biomass at harvest in the mixed-species stand. While NPP partitioning in eucalypt monoculture was more in favor of aboveground growth at the Brazilian site than at the Congolese site, NPP partitioning of the mixed-species stands was shifted towards aboveground growth at Kissoko and towards belowground growth at Itatinga. Mixed-species plantations of eucalypt and acacia are potentially a valuable option where eucalypt growth is limited by N availability, but might fail to increase NPP in locations where other factors such as water availability are limiting growth. Comparing water use and water use efficiency for wood production in mixed-species plantations in contrasted environments will be a step forward in our understanding of species interactions that is required for improving management techniques for a sustainable wood production in tropical areas.

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