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## *Eucalyptus* and *Acacia* tree growth over entire rotation in single- and mixed-species plantations across five sites in Brazil and Congo

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## ABSTRACT

The association of N<sub>2</sub>-fixing species (NFS) could be an attractive option for achieving a sustainable increase of *Eucalyptus* plantations (EP) productivity through a positive balance between facilitative effects and competition between species. A randomised block design was replicated at four sites (Cenibra, USP, Suzano and IP) in Southern Brazil and at one site in Congo. The development of mono-specific stands of *Acacia mangium* (100A) and *Eucalyptus grandis* or *urophylla* × *grandis* (100E), was compared with N fertilisation treatment (100E + N) and with mixed-species plantations in a 1:1 ratio (50A:50E), and in an additive series with varying densities of acacia for the same density of eucalypt (25A:100E, 50A:100E, 100A:100E). The objectives were to assess the effect of mixtures on tree growth and stand production, and the behaviour of the two species in contrasting soil and climatic conditions. Tree growth was monitored over stand rotation and the biomass of aboveground tree components estimated at mid-rotation and at harvesting age. *Eucalyptus* height was 13% higher in Brazil than in Congo. Favourable ecological conditions in Congo and Cenibra led to 50% higher *Acacia* tree height than at the other sites. A depressive effect of *Eucalyptus* neighbour trees on *Acacia* height and circumference growth, lower in Congo than in Brazil, was observed in the mixtures from age 1–2 years onwards. Depressive effects of acacia on eucalypt height and circumference growth were low in USP, Suzano and IP, high in Cenibra, and not observed in Congo, in 50A:50E and 25A:100E. A positive though insignificant response to N fertilisation was only found in USP and Congo. Complementarity for light and soil resource capture between *Eucalyptus* and *Acacia* trees resulted in mean annual increments in total stand stemwood biomass (MAI) that were 7–15%, 6–12%, and 40% higher in the additive series than for 100E in Cenibra, USP and Congo, respectively at mid-rotation. Whilst lasting complementarity and facilitation in Congo led to 17–34% higher MAI in mixtures than for 100E at harvesting age, MAIs were not significantly higher in mixtures than for 100E in Brazil. Mixed-species plantations of *Eucalyptus* and *A. mangium* might enhance aboveground stand production on poor nutrient soils in warm and humid tropical climates with low water limitations.

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### 1. Introduction

The area of *Eucalyptus* plantations (EP) now covers about 20 million hectares in the world (GIT, 2009). One reason for their expansion is the growing demand in eucalypt pulp, which increased from 2 million tons in 1980 to 18 million tons in 2010

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(FAO, 2010). However, with the increase in the human population and the competition for arable land, they are often established on poor soils (Evans and Turnbull, 2004) and/or outside their optimal climatic zones (Alfenas et al., 2011). In addition, their expansion may be limited by conflicts for land use with local populations (Cossalter and Pye-Smith, 2003). A sustainable increase in production per unit area of EP is thus needed to meet the market demand in the medium and long term. Special attention should be given to nitrogen (N) and phosphorus (P) requirements (Peñuelas et al., 2012) because they are both likely to limit tree growth in commercial EP (Corbeels et al., 2005; Gonçalves et al., 2008; Laclau et al., 2010a). Nitrogen and P inputs are required to sustain EP production although the use of inorganic fertilisers should be limited in the future because of their rising costs: a four- and sixfold increase has been observed in the last decade for urea and triple super phosphate, respectively (<http://siteresources.worldbank.org>).

Planting N<sub>2</sub>-fixing species (NFS) in EP could be an alternative to monocultures because mixed-species ecosystems may be more productive than *Eucalyptus* monocultures (Binkley et al., 2003; Forrester et al., 2006, 2010; Richards et al., 2010). The association of NFS with eucalypts is likely to enhance the availability of N through N<sub>2</sub> fixation (Bouillet et al., 2008; Adams et al., 2010), higher litter fall production (Forrester et al., 2005a; Laclau et al., 2008), greater leaf decomposition and N cycling (Forrester et al., 2005a; Xiang and Bauhus, 2007) and/or higher soil N mineralisation (Voigtlaender et al., 2012). Moreover, the availability of inorganic soil P may increase (Forrester et al., 2005a,b; Boyden et al., 2005; Hinsinger et al., 2011) through the production of phosphatase enzymes, which are compulsory for mobilising organic P (Binkley et al., 2000; Houlton et al., 2008). However, some studies have shown that NFS have no effect or a depressive influence on the growth of *Eucalyptus* trees and overall stand productivity (Moraes de Jesus and Brouard, 1989; Snowdon et al., 2003; Forrester et al., 2005b).

Whether or not a mixture may outperform *Eucalyptus* monocultures depends on the balance between competitive and facilitative processes (Vandermeer, 1989; Friedley, 2001). Competition between species may occur above ground for light (Austin et al., 1997; Hunt et al., 2006) and/or belowground for water and nutrients (Boyden et al., 2005; Silva et al., 2009). Facilitative processes primarily include facilitation, whereby one species increases the availability of resources for another (e.g. N and P), and modification of the environment (e.g. more rapid canopy closure or use of cover crops reducing weed development; Little et al., 2002). The second facilitative process is that of complementarity, which leads to a more complete capture of resources than in monocultures and/or reduced competition through niche partitioning (e.g. canopy stratification; Hunt et al., 2006; Laclau et al., 2008), although this pattern is not always the case (e.g. more complete soil exploration without root stratification; Bauhus et al., 2000).

A review on mixed-species *Eucalyptus* plantations with NFS (Forrester et al., 2006) showed that the mean annual increment of stemwood biomass (MAI) for mono-specific eucalypt stands ranged from 3 Mg ha<sup>-1</sup> year<sup>-1</sup> to 16 Mg ha<sup>-1</sup> year<sup>-1</sup> when mixtures outperformed monocultures. However, MAI in productive commercial EP range from 20 to 30 Mg ha<sup>-1</sup> year<sup>-1</sup> in Brazil owing to the use of genetically improved material, high fertiliser applications and effective weed control (Stape et al., 2010). Intra- and inter-specific competition is, thus, likely to differ considerably from patterns found in less productive stands. It should also be emphasised that only 20% of the experiments analysed by Forrester et al. (2006) included N-fertilised *Eucalyptus*. Replacement series (i.e. testing various proportions of *Eucalyptus* and NFS for the same total stand density) that confound inter-specific interactions with changes in spacing between the trees have been used systematically. However, a combination of replacement and additive designs

(i.e. the density of *Eucalyptus* remains constant while that of the NFS varies) is needed so that the intra-specific and inter-specific interactions can be quantified correctly (Sackville Hamilton, 1994; Kelty and Cameron, 1995). A combination of this kind was tested in Itatinga (Brazil – SP) to compare mono-specific stands of *Eucalyptus grandis* (Hill ex Maid) and *Acacia mangium* (Wild) with mixed-species plantations in a 1:1 ratio, and other stands with different densities of acacias for the same density of eucalypts (Laclau et al., 2008). *Acacia* trees were suppressed in mixed-species stands from age 12 months onwards and did not influence biomass production and partitioning within eucalypts. At 30 months of age, this pattern led in mixture combining the two species with *A. mangium* planted in the additive series at a density of 50% of the eucalypts to total stand biomass accumulation 10% higher than in pure *Eucalyptus* stand. Facilitative and competitive processes may depend on resource availability, with higher competition in fertile environments and greater facilitation under harsh conditions (Bertness and Callaway, 1994; Paquette and Messier, 2011). The balance between these processes may also vary as stands develop (Forrester et al., 2011). Therefore, our experimental design was duplicated at various sites in Brazil and Congo to cover a large range of ecological conditions. The trial was monitored over a full stand rotation. As far as we know it was the first network on mixed-species plantations of *Eucalyptus* and NFS duplicating the same experimental design. That gave the opportunity to assess the effect of mixtures of *E. grandis* (or *Eucalyptus urophylla* (S.T. Blake) × *E. grandis*) and *A. mangium* on tree growth and stand production in contrasting soil and climatic conditions. Our hypothesis was that the balance between facilitative and competitive processes changes with age and is more favourable at the less productive sites.

## 2. Material and methods

### 2.1. Study sites

Our study was carried out at four sites in South-East Brazil and one site in the coastal plain of the Congo where there are large commercial plantations of *E. grandis* and *E. urophylla* × *E. grandis* (Table 1). The mean annual rainfall ranged from 1130 mm to 1420 mm. These sites covered a relatively large range of mean temperatures (from 19.0 °C in USP to 25.7 °C in Congo), mean atmospheric humidity (from 65–71% in Brazil to 81% in Congo) and dry season duration (from 2 months in USP and Suzano to 4 months in Congo) for intensively-managed tropical eucalypt plantations. The soils were Ferralsols at the USP, Cenibra and Suzano sites and Ferralic arenosols at the International Paper (IP) and Congo sites (FAO classification). The pH was acidic (between 4.5 and 5.8) and the amounts of available nutrients in the soils were low at all the sites, decreasing sharply with soil depth. The soils differed in texture, with clay contents ranging from 10–15% in Congo and IP to 50–70% in Cenibra. The soils were more depleted in N and less in P in Congo than at all other sites (Table 1).

### 2.2. Experimental design

The experiments were set up in former *Eucalyptus* stands that had been managed for 20–60 years when our trials were established (Table 2). The same experimental design was replicated in all the sites. The treatments were:

- 100A. Pure *A. mangium* stand;
- 100E. Pure *Eucalyptus* stand, with no N fertilisation, except in Congo where 54 g N *Eucalyptus* tree<sup>-1</sup> was applied at planting;
- 100E + N. Pure *Eucalyptus* stand, with N fertilisation;

**Table 1**  
Main site characteristics. Soil properties are given for (0–5 cm), (50–100 cm) and (200–300 cm) layers. Standard deviations are given in brackets ( $n = 3$ ).

Company site	Latitude Longitude (°C)	Mean T <sup>re</sup> (°C)	Length dry season <sup>a</sup>	Mean air humidity (%)	Annual rainfall (mm)	Soil type <sup>b</sup> clay content (%)	Organic matter (%)	Total N <sup>f</sup> (g kg <sup>-1</sup> )	pH water	Exc. bases (cmol <sub>c</sub> kg <sup>-1</sup> soil)	CEC (cmol <sub>c</sub> kg <sup>-1</sup> soil)	Available P <sup>g</sup> (mg kg <sup>-1</sup> )
Cenibra	19°16S	24.4	3 months	71	1240	Ferralsols 50.7 (2.7) <sup>c</sup>	3.8 (0.8) <sup>f</sup>	1.70 (0.36) <sup>f</sup>	5.5 (0.5) <sup>f</sup>	5.78 (4.64) <sup>f</sup>	10.75 (4.96) <sup>f</sup>	6.3 (2.5) <sup>f</sup>
Santana do Paraiso (MG) Brazil	41°47 W					68.7 (4.1) <sup>d</sup>	1.2 (0.2) <sup>d</sup>	n.d. <sup>d</sup>	4.7 (0.3) <sup>d</sup>	0.14 (0.02) <sup>d</sup>	3.79 (0.43) <sup>d</sup>	1.0 (0.0) <sup>d</sup>
						68.6 (2.5) <sup>e</sup>	0.1 (0.0) <sup>e</sup>	n.d. <sup>e</sup>	5.0 (0.3) <sup>e</sup>	0.16 (0.01) <sup>e</sup>	2.15 (0.43) <sup>e</sup>	<1 <sup>e</sup>
Suzano	23°11S	21.4	2 months	71	1420	Ferralsols 11.8 (1.4) <sup>c</sup>	2.4 (0.5) <sup>f</sup>	0.84 (0.20) <sup>f</sup>	4.5 (0.2) <sup>f</sup>	0.40 (0.21) <sup>f</sup>	5.87 (0.19) <sup>f</sup>	11.3 (7.8) <sup>c</sup>
Bofete (SP) Brazil	48°25 W					16.8 (1.4) <sup>d</sup>	0.5 (0.1) <sup>d</sup>	n.d. <sup>d</sup>	4.6 (0.3) <sup>d</sup>	0.11 (0.00) <sup>d</sup>	1.90 (0.43) <sup>d</sup>	<1 <sup>d</sup>
						19.3 (1.3) <sup>e</sup>	0.1 (0.1) <sup>e</sup>	n.d. <sup>e</sup>	5.1 (0.1) <sup>e</sup>	0.11 (0.00) <sup>e</sup>	0.85 (0.22) <sup>e</sup>	<1 <sup>e</sup>
USP	23°02S	19	2 months	70	1390	Ferralsols 11.4 (0.7) <sup>c</sup>	3.5 (0.8) <sup>f</sup>	0.91 (0.18) <sup>f</sup>	5.5 (0.2) <sup>f</sup>	0.96 (0.23) <sup>f</sup>	1.76 (0.27) <sup>f</sup>	3.1 (0.3) <sup>c</sup>
Itatinga (SP) Brazil	48°37W					16.1 (0.0) <sup>d</sup>	0.7 (0.0) <sup>d</sup>	0.24 (0.01) <sup>d</sup>	5.8 (0.3) <sup>d</sup>	0.02 (0.00) <sup>d</sup>	0.58 (0.01) <sup>d</sup>	1.0 (0.2) <sup>d</sup>
						16.1 (0.0) <sup>e</sup>	0.4 (0.0) <sup>e</sup>	0.14 (0.01) <sup>e</sup>	5.7 (0.1) <sup>e</sup>	0.02 (0.01) <sup>e</sup>	0.21 (0.04) <sup>e</sup>	1.5 (0.2) <sup>e</sup>
International Paper Luiz Antônio (SP) Brazil	21°35S 47.31 W	23.3	3 months	65	1420	Ferralsols 10.1 (2.5) <sup>c</sup>	1.7 (0.3) <sup>f</sup>	0.64 (0.12) <sup>f</sup>	4.8 (0.1) <sup>f</sup>	0.84 (0.12) <sup>f</sup>	4.32 (0.08) <sup>f</sup>	14.0 (4.6) <sup>c</sup>
						12.6 (2.5) <sup>d</sup>	0.4 (0.1) <sup>d</sup>	n.d. <sup>d</sup>	4.8 (0.2) <sup>d</sup>	0.13 (0.04) <sup>d</sup>	1.98 (0.27) <sup>d</sup>	1.7 (0.6) <sup>d</sup>
						13.9 (2.3) <sup>e</sup>	0.2 (0.0) <sup>e</sup>	n.d. <sup>e</sup>	4.8 (0.2) <sup>e</sup>	0.11 (0.00) <sup>e</sup>	1.02 (0.05) <sup>e</sup>	<1 <sup>e</sup>
CRDPI	4°41S	25.7	4 months	81	1130	Ferralsols 7.7 (1.2) <sup>c</sup>	1.14–1.71 <sup>c</sup>	0.46 (0.11) <sup>f</sup>	4.6– 4.8 <sup>c</sup>	0.23–0.30 <sup>c</sup>	0.53–0.69 <sup>c</sup>	15.23 <sup>c</sup>
Pointe-Noire Congo	12°01E					9.8 (0.5) <sup>d</sup>	0.33–0.47 <sup>d</sup>	0.13 (0.07) <sup>d</sup>	4.9– 5.5 <sup>d</sup>	0.10–0.13 <sup>d</sup>	0.29–0.35 <sup>d</sup>	7.24 <sup>d</sup>
						11.3 (0.5) <sup>e</sup>	0.195 <sup>e</sup>	0.07 (0.01) <sup>e</sup>	5.15 <sup>e</sup>	0.125 <sup>e</sup>	0.315 <sup>e</sup>	3.55 <sup>e</sup>

<sup>a</sup> Mean monthly rainfall < 30 mm.

<sup>b</sup> FAO classification.

<sup>c</sup> [0–5 cm] layer.

<sup>d</sup> [50–100 cm] layer.

<sup>e</sup> [200–300 cm] layer; n.d. not determined.

<sup>f</sup> Total N determined by elementary CHN analyser Fisons/Carlo Erba NA 2000 (Milan, Italy).

<sup>g</sup> Available P determined by Mellich-1 and colorimetry. Only one profile for P determination at CRDPI site.

**Table 2**  
Main trial characteristics.

Company site	Species	Planting date	Spacing <sup>a</sup> (m × m)	Stand density <sup>a</sup> (trees ha <sup>-1</sup> )	Total plot size (trees)	Inner plot size (trees)	Blocks <sup>b</sup>	Fertilisation at planting <sup>c</sup> (N, P, K; g plant <sup>-1</sup> ) (Limestone, dolomite, boiler ash; kg ha <sup>-1</sup> ) All treatments	Fertilisation after planting <sup>c</sup> (total kg ha <sup>-1</sup> ) Application dates (months) All treatments	Added N (total kg ha <sup>-1</sup> ) Application dates (months) 100E + N treatment	Previous land uses <sup>d</sup>
Cenibra Santana do Paraíso (MG) Brazil	<i>E. urophylla</i> × <i>E. grandis</i>	11/2004	3 × 3	1111	10 × 10	6 × 6	4	N: 5; P: 12; K: 5 Cu, B, Zn Dolomite: 1500	P: 31 K: 157 (2) N: 106 (1, 11)	<1960: cerrado 1960–2004: <i>Eucalyptus</i> sp	
Suzano	<i>E. grandis</i>	02/2005	3 × 2	1666	8 × 10	4 × 6	4	N: 9; P: 22; K: 14 B, S Boiler ash: 3000	K: 163 (6, 10, 12, 24) N: 167 (6, 12, 22)	<1972: pasture 1972–2004: <i>Eucalyptus</i> sp.	
Bofete (SP) Brazil USP Itatinga (SP) Brazil	<i>E. grandis</i>	05/2003	3 × 3	1111	10 × 10	6 × 6	4	P: 40; K: 9 B, Fe, Zn, Mn Limestone: 2000	K: 75 (6, 12, 18) N: 120 (0, 6, 12, 18)	<1940: cerrado 1940–1988: <i>E. saligna</i> 1988–2002: <i>E. grandis</i>	
Int. Paper Luiz Antônio (SP) Brazil CRDPI Pointe-Noire Congo	<i>E. urophylla</i> × <i>E. grandis</i> <i>E. urophylla</i> × <i>E. grandis</i>	02/2005 05/2004	3 × 3 3.75 × 3.33	1111 801	10 × 10 10 × 10	6 × 6 6 × 6	4 5	N: 4; P: 26; K: 5 Cu, Zn, B Dolomite: 1200 N: 43	K: 141 (6, 12, 18) N: 43 (12)	N: 13 (3) N: 43 (12)	<1982: cerrado 1982–2004: <i>E. grandis</i> <1984: savannah 1984–2004: <i>Eucalyptus</i> sp.

<sup>a</sup> In monocultures (100A, 100E, 100E + N) and in 50A:50E.

<sup>b</sup> In Congo, one block was used for biomass estimation at 34 months; for the 4 remaining blocks we analysed the only plots with survival rate >70% for *Acacia* and *Eucalyptus* at 77 months of age: 100A (2 blocks – mean survival rate of 78%); 50A:50E (2 blocks – mean survival rate of 83% for *Acacia* and 89% for *Eucalyptus*); 50A:100E (3 blocks – mean survival rate of 93% for *Acacia* and 75% for *Eucalyptus*); 100E (4 blocks – mean survival rate of 90%); 100E + N (4 blocks – mean survival rate of 92%); 25A:100E (4 blocks – mean survival rate of 94% for *Acacia* and 89% for *Eucalyptus*).

<sup>c</sup> Cenibra. At planting: NPK (6–30–6); after planting: P (superphosphate), K (potassium chloride), Suzano. At planting: NPK (6–30–10); after planting: N (ammonium nitrate); K (potassium chloride). USP. N (ammonium nitrate); P (superphosphate); K (potassium chloride). Int. Paper. At planting: NPK (4–28–6) and P (superphosphate); after planting: K (potassium chloride). CRDPI. N (ammonium nitrate), only on *Eucalyptus* trees. Fertilizers placed in holes at 20–30 cm of each tree at planting; fertilizers broadcasted after planting. No singling or thinning during stand rotation.

<sup>d</sup> The trees of the previous stand rotation were devitalized on all the sites using an application of glyphosate; only the boles (stemwood + stem bark) were removed from the plots and harvest residues were spread uniformly in the field.

25A:100E. 100E + *A. mangium* planted in mixture at a density of 25% of the *Eucalyptus* density;  
50E: 100E. 100E + *A. mangium* planted in mixture at a density of 50% of the *Eucalyptus* density;  
100A:100E. 100E + *A. mangium* planted in mixture at a density of 100% of the *Eucalyptus* density; this treatment was not tested in Congo.

For these three treatments *Acacia* seedlings were planted at mid-distance between eucalypts in the same planting rows.

50A:50E. Mixture at a 1:1 ratio between *Eucalyptus* and *A. mangium* (replacement treatment). The two species were planted alternately in the row, and between adjacent rows.

Total tree densities were similar in 100A, 100E, 100E + N, and 50A:50E in each experiment. However, they varied from 801 stems ha<sup>-1</sup> in Congo, to 1111 stems ha<sup>-1</sup> in Cenibra, USP and Suzano and 1666 stems ha<sup>-1</sup> in Suzano. These densities that reflect the current densities in commercial plantations lead to the maximum stemwood production in *Eucalyptus* monocultures at each site. Increasing the stocking density of *Eucalyptus* trees do not then lead to higher MAIs both in Congo (UR2PI, 2007) and in Brazil (Gonçalves et al., 2008). Fertiliser inputs on the Brazilian sites did not limit tree growth (Laclau et al., 2008; Stape et al., 2010), with the possible exception of N in all the treatments apart from 100E + N. N fertilisation was applied at planting in all treatments in Congo to obtain early *Eucalyptus* tree growth compatible with that found in commercially managed plantations (Bouillet et al., 2004). Additional N fertilisation was applied the first year after planting in 100E + N.

### 2.3. Stand growth and above-ground biomass accumulation

Tree growth was monitored up to the end of stand rotation in all treatments. Height and circumference at breast height were measured excluding two buffer rows in each plot at various ages throughout stand rotation up to harvesting age (about 6 years of age). Most of the acacias were multi-stem trees and the circumference of all the stems with a diameter at breast height >2 cm was measured on each inventory. For multi-stem trees, the basal area at breast height was cumulated for all the stems for each tree and an “equivalent circumference” was calculated.

Above-ground biomass was estimated by sampling 10 trees of each species distributed over the range of tree basal areas in 100A, 100E and 50A:50E at 66, 63, 72, 73 and 77 months after planting at the Cenibra, Suzano, USP, IP and Congo sites, respectively. The same sampling was also carried out at age 30 months at the USP site. In addition, 10 trees per species were sampled in 50A:100E at 30 and 72 months after planting in USP, and in 100A, 100E and 50A:100E at 34 months after planting in Congo. The trees were separated into components: leaves, living branches, dead branches, stemwood and stem bark. The stem of each tree was sawn into 3 m sections. Diameters, lengths and masses were measured in the field, as well as the circumference over and under bark at 1 m intervals. The foliage was collected from three different sections of the trees' crown. Sub-samples of each component were dried at 65 °C to constant weight. Site-specific biomass equations were established (Table 4 in Appendix). The allometric relationships established at age 30 months in USP (Laclau et al., 2008) were applied at 31, 27 and 22 months of age in the Cenibra, Suzano and IP experiments, respectively. The biomass equations established for *Acacia* trees in 50A:100E were used in 25A:100E and 100A:100E in USP. At the harvesting age on the other sites, the equations established in 100E were applied for *Eucalyptus* trees in the additive series of the same experiment and in the 100E + N treatment. The models fitted for *Acacia* trees in 50A:50E were used in 25A:100E, 50A:100E and 100A:100E. The allometric relationships established in 100E at 34 months of age in Congo were used



at this age for *Eucalyptus* trees in the additive series of the same experiment and in the 100E + N treatment. The biomass equations established at this age for *Acacia* trees in 100A and 50A:100E were applied in 100A, and 25A:100E and 50A:50E, respectively.

#### 2.4. Statistical analysis

Differences between treatments and blocks for tree and stand characteristics were tested at each site and each stand age using a two-way ANOVA. The GLM procedure of SAS 9.3 was used (SAS Institute, Cary, NC, USA). Homogeneity of variances was tested at each age and at each site by Levene's test and original values were transformed when variances were unequal. The probability level used to determine significance was  $P < 0.05$ . When the ANOVA indicated significant effects, the means were compared with Bonferroni's test. The PDIF statement of PROC GLM was used in Congo where plots were excluded from the trial when tree survival was  $< 70\%$ . The number of plots used in the analysis for each experiment is indicated at the bottom of Table 2.

The methodology used to establish biomass equations was described by Laclau et al. (2009). In brief, the models were fitted for each component of each species at every age and every site. Fittings were performed using PROC NLP of the SAS 9.3 software and maximum likelihood estimations were used with Akaike Information Criterion (AIC) to select the individual models per treatment, per site and per age or a global model for the two treatments of each site and at each age. Final models were applied to the stand inventory at each age and at each site to assess the biomass of each component.

### 3. Results

#### 3.1. Survival rates

At the end of stand rotation, eucalypt survival ranged from 92% to 100%, 97% to 100%, 84% to 96%, and 94% to 98% at the Cenibra, USP, Suzano and IP sites, respectively. The corresponding values for *A. mangium* growing in mixtures were 86–97%, 93–99%, 75–

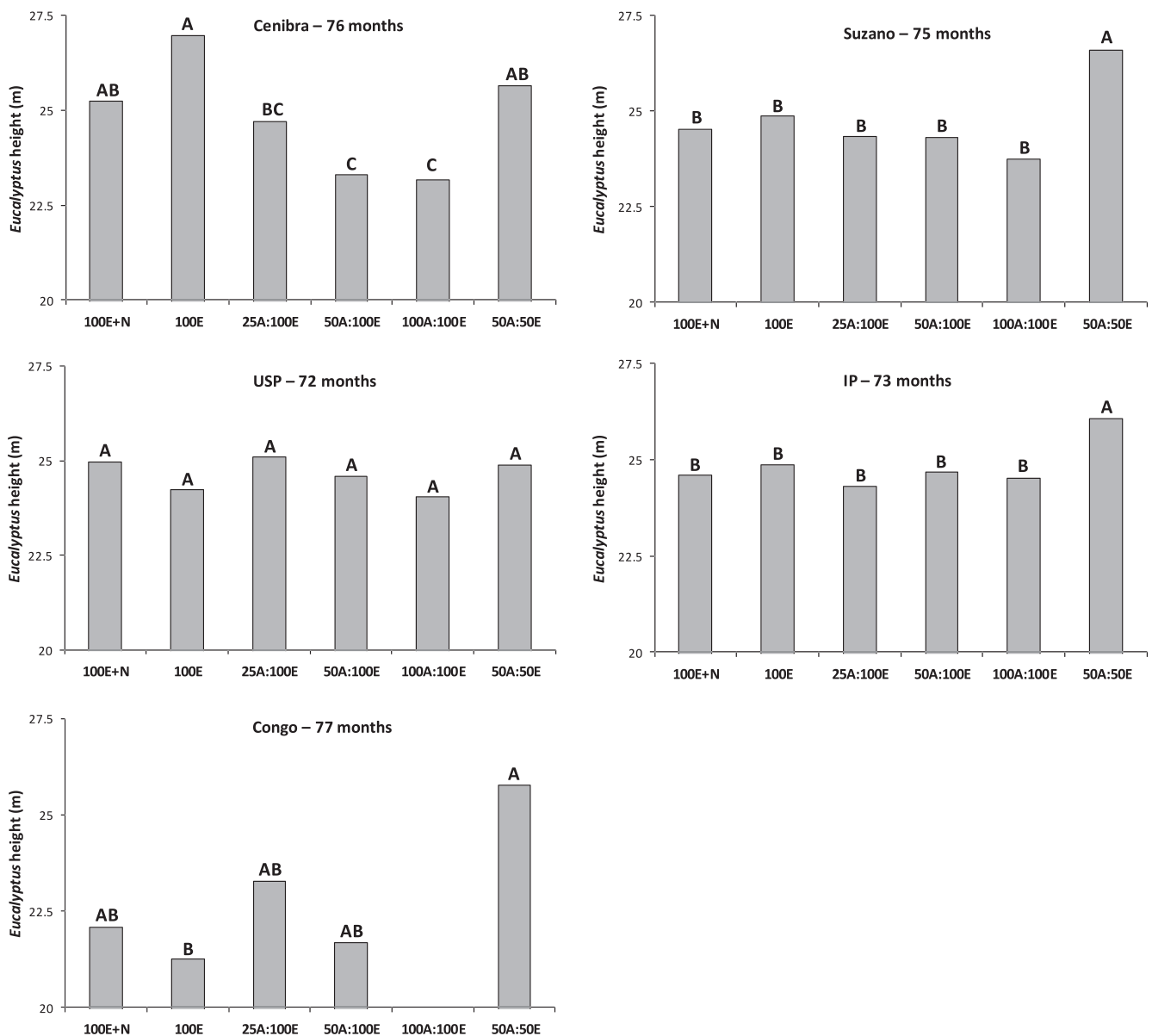


Fig. 1. Mean *Eucalyptus* tree height in Cenibra (76 months), Suzano (75 months), USP (72 months), IP (73 months) and Congo (77 months). Different letters indicate significant differences between treatments ( $P < 0.05$ ).

94%, and 75–90%, respectively. Tree survival in 100A was 96% and 89% in USP and Suzano, respectively. Owing to windthrown trees, this rate dropped in 100A to 47% and 67% in Cenibra and IP, respectively. In Congo, tree survival rates were low in some plots from 12 months after planting onwards probably due to bacterial wilt caused by *Ralstonia solanacearum* (Roux et al., 2000). In the other plots survival at the end of rotation ranged from 75% to 92% and from 78% to 94% for *Eucalyptus* and *Acacia*, respectively (Table 2). Tree mortality did not vary with the proportion of *Acacia* in the mixture, for both species and regardless of the site.

### 3.2. Stand growth

#### 3.2.1. Height growth

*Eucalyptus* height growth was 13% higher in Brazil than in Congo, with mean annual increments at the end of stand rotation of  $4.0 \text{ m year}^{-1}$  and  $3.6 \text{ m year}^{-1}$ , respectively. No significant positive effects of N fertilisation were observed on *Eucalyptus* height at the end of stand rotation at any of the sites (Fig. 1). We found a significantly higher *Eucalyptus* height (+2.6 m) in 100E than in the other treatments of the additive series (nA:100E = 25A:100E, 50A:100E and 100A:100E) in Cenibra only, with a tendency of lower eucalypt growth with increasing acacia density. Eucalypt height was significantly higher in 50A:50E than in additive treatments in Suzano, IP and Congo, with mean differences at the end of stand rotation of 2.3, 1.5 and 3.7 m, respectively.

Mean *Acacia* height increments were 2.9 and  $2.7 \text{ m year}^{-1}$  in Cenibra and Congo, respectively, with height values ranging between 16.2 and 20.3 m at harvesting age (data not shown). *Acacia mangium* tree heights were not significantly different between treatments over stand rotation, except in 100A:100E in Cenibra where *Acacia* growth was significantly lower than in the other treatments at 55 and 66 months of age. *Acacia* trees exhibited lower growth at the USP, IP and Suzano sites than in Cenibra and Congo. Mean *Acacia* tree height 6 years after planting for these three sites was 10.5 m in nA:100E, 11.8 m in 50A:50E and 15.2 m in 100A. Differences between treatments increased throughout stand rotation.

In Brazil, acacias were overtopped by eucalypts at an early stage of stand development. The difference in height between the two species was  $>4 \text{ m}$  from 18 to 24 months onwards (Fig. 2), and ranged from 6.1 m to 16.1 m at the end of stand rotation, with a mean value of 12.5 m and 11.7 m in the additive treatments and in 50A:50E, respectively. Canopy stratification appeared later in Congo with a mean difference in height between the two species of 5.3 m and 7.6 m at 77 months of age in the additive treatments and 50A:50E, respectively.

#### 3.2.2. Circumference growth

Mean *Eucalyptus* circumferences were slightly higher over the rotation in 100E + N than in 100E in USP and Congo, even though the two treatments were only significantly different at the USP site at 12 and 17 months of age (Fig. 3). In Cenibra only, *Eucalyptus* circumferences significantly decreased with the number of trees in the additive treatments. The mean differences, at 76 months of age, between 100E and 50A:100E, and 100A:100E were of +5.6 and +6.7 cm, respectively. Eucalypts rapidly exhibited significantly higher circumferences in 50A:50E than in the other treatments at all sites. The differences in mean eucalypt circumference between 50A:50E and the other treatments increased with tree age and ranged from 6.6 cm in Cenibra to 12.9 cm in Congo at the end of stand rotation.

In Cenibra, *Acacia* circumferences significantly decreased in the additive treatments as the total stand density increased (Fig. 4). At the other Brazilian sites, the lowest *Acacia* circumferences were observed in the additive treatments. Differences between 100A:100E

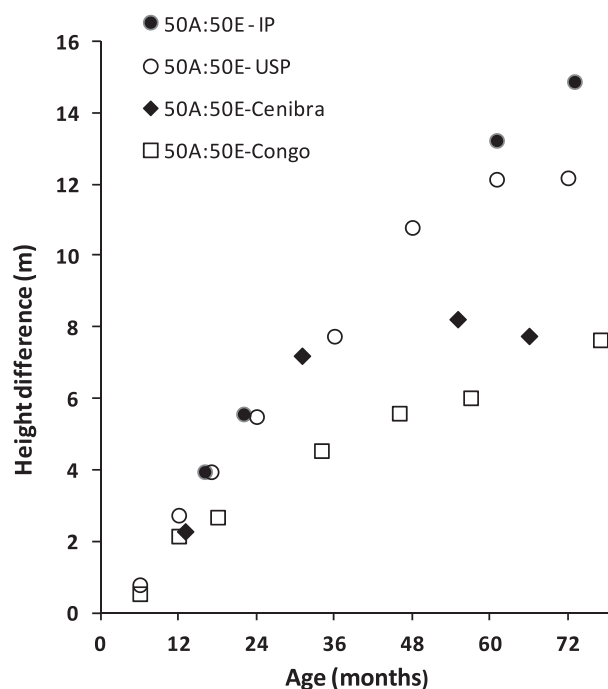


Fig. 2. Difference between *Eucalyptus* and *Acacia* tree height over 50A:50E rotation in IP, USP, Cenibra and Congo. The results were similar in USP and Suzano sites.

and the two other treatments of the additive series (25A:100E and 50A:100E) were only significant in Suzano. In Congo, acacia circumference was not higher in 100A than in the additive treatments. *Acacia* circumference was similar in 100A and 50A:50E in Cenibra and Congo, showing that the influence of neighbouring acacia or eucalypt on *Acacia* tree growth was of the same order of magnitude. By contrast, *Acacia* circumference was significantly higher in 100A than in 50A:50E at the other Brazilian sites.

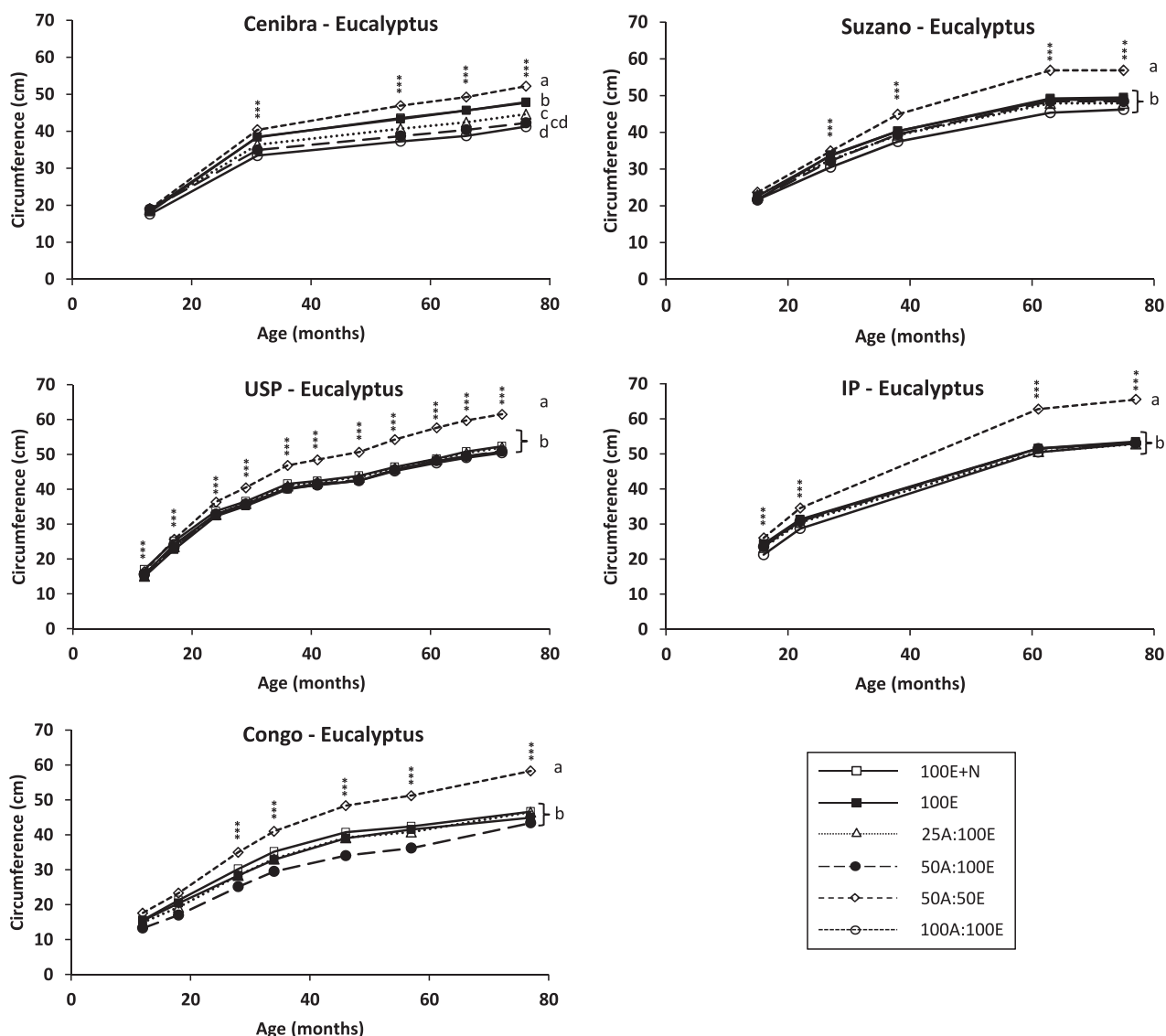
### 3.3. Biomass

#### 3.3.1. Stemwood production

*Eucalyptus* stemwood production in 100E was on average 2.7 times higher in Brazil than in Congo with MAI at harvesting age of 20.5 and  $7.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$ , respectively. In USP and Congo, we observed 8–15% and 7% higher MAI in 100E + N than in 100E at the beginning of the stand rotation (about 30 months of age) and harvesting age, respectively. *Acacia* MAI in 100A was of 9.8 and  $6.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$  at harvesting age in Brazil and Congo, respectively. The lowest production in 100A was observed in IP with MAI of  $4.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$  at 77 months of age. The highest stemwood production of *Acacia* trees compared to *Eucalyptus* trees was found in Congo with a ratio between MAIs in 100A and 100E of 151% and 86% at 34 months and 77 months after planting, respectively.

At the beginning of the stand rotation, higher MAIs were found in nA:100E than in 100E in Cenibra, USP and Congo, with an increase in stemwood biomass of 7–15%, 6–12% and approximately 40%, respectively (Fig. 5 and Table 5 in Appendix). At harvesting age, MAIs of nA:100E were similar to those found in *Eucalyptus* monocultures at the Brazilian sites (Fig. 6 and Table 6 in Appendix). By contrast, 25A:100E and 50A:100E in Congo were 34% and 17% more productive than 100E, respectively. At this site, 50A:50E exhibited an MAI 71% and 31% higher than in 100E at 34 and 77 months after planting, respectively.

In Brazil, we observed a pattern of lower *Eucalyptus* production with an increase in acacia density in the mixtures, except at the IP



**Fig. 3.** Time course of mean *Eucalyptus* circumference over stand rotation depending on sites. Significant differences between at least two treatments ( $P < 0.001$ ) are indicated by \*\*\*. Different letters indicate significant differences between treatments ( $P < 0.05$ ) at the last date of measurement.

site. At harvesting age, *Eucalyptus* MAI was 34%, 14% and 6% lower in 100A:100E than in 100E, in Cenibra, Suzano and USP, respectively. In Congo, we observed that *Acacia* trees had a significant depressive effect on *Eucalyptus* production in the additive series in 50A:100E only, where eucalypts were 21% less productive than in 100E at 77 months of age. Eucalypts always exhibited lower MAIs per hectare in 50A:50E than in the additive treatments as a result of their 50% lower stocking density. At the end of stand rotation, eucalypt stemwood MAIs for 50A:50E were 35%, 30%, 33%, 20% and 15% lower in Cenibra, Suzano, USP, IP and Congo than for 100E, respectively.

In Brazil, individual *Acacia* stemwood biomass was lowered considerably by *Eucalyptus* neighbours, as well as by intra-specific competition. At the end of stand rotation, the average difference with 100A was -68%, -75%, -85% and -61% in 25A:100E, 50A:100E, 100A:100E and 50A:50E, respectively. The depressive effect of *Eucalyptus* trees on *Acacia* production was much less marked in Congo. The differences in individual *Acacia* stemwood were +28%, -24% and -19% in 25A:100E, 50A:100E and 50A:50E, respectively.

### 3.3.2. Biomass of harvest residues

The biomass of small tree components kept on-site at clear cutting (harvest residues) was higher in 100A than in 100E and 100E + N, except in IP where *Acacia* growth was very poor (Table 3). Mixing *Acacia* trees with *Eucalyptus* trees led to residue biomasses 50–78%, 12–80%, 10–30%, 2–19%, and 59–93% higher than in pure eucalypt stands in Cenibra, Suzano, USP, IP and Congo, respectively (Table 3).

## 4. Discussion

### 4.1. Species adaptation and ecological interactions

Species adaptation to site characteristics was partially responsible for inter-specific interactions. We observed that *Eucalyptus* trees have a depressive effect on *Acacia* tree growth from 1–2 years after planting onwards, which is lower in Congo than at the Suzano, USP and IP sites. We also found that there was less competition between *A. mangium* and *Eucalyptus* in USP, Suzano and IP



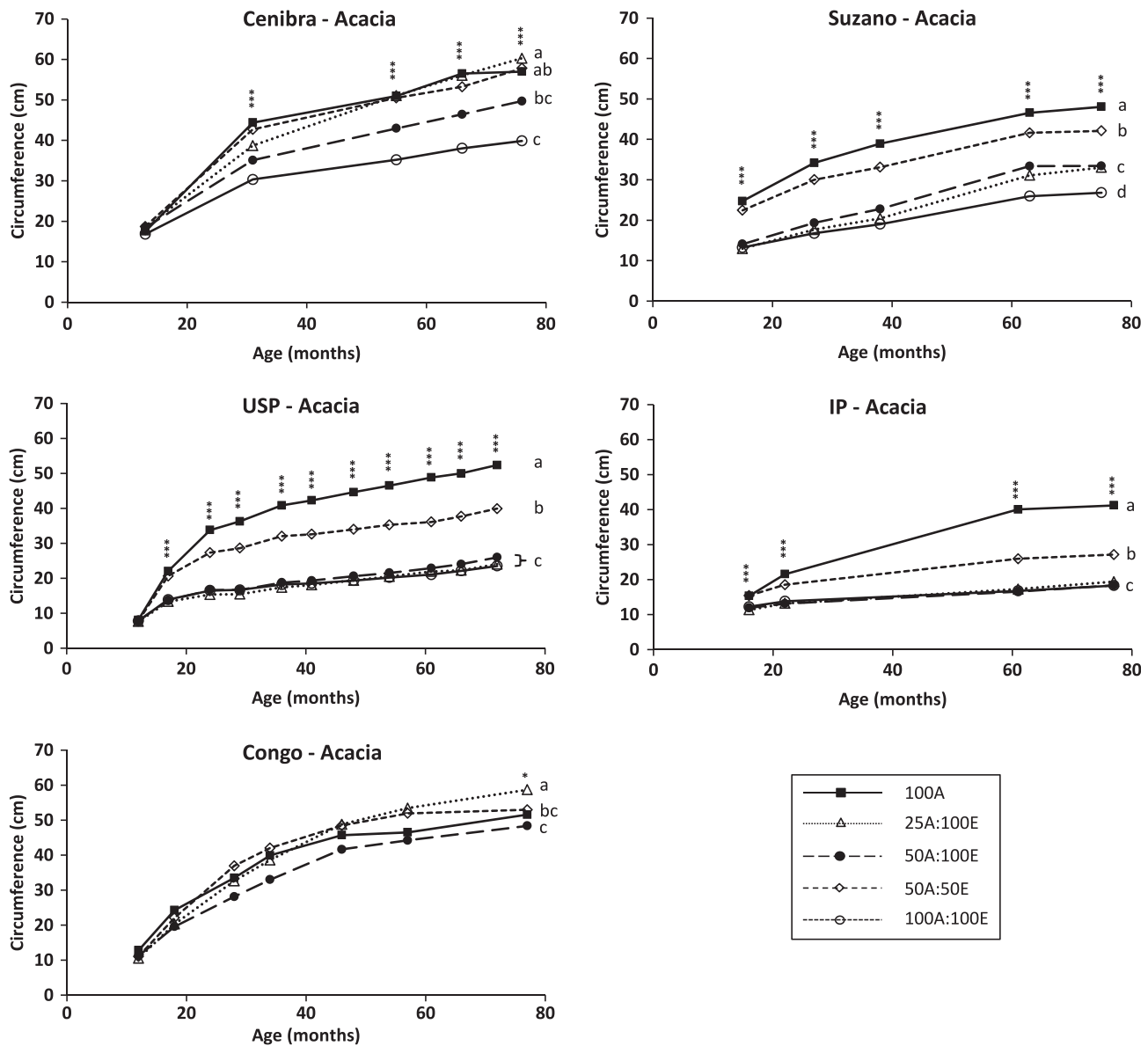
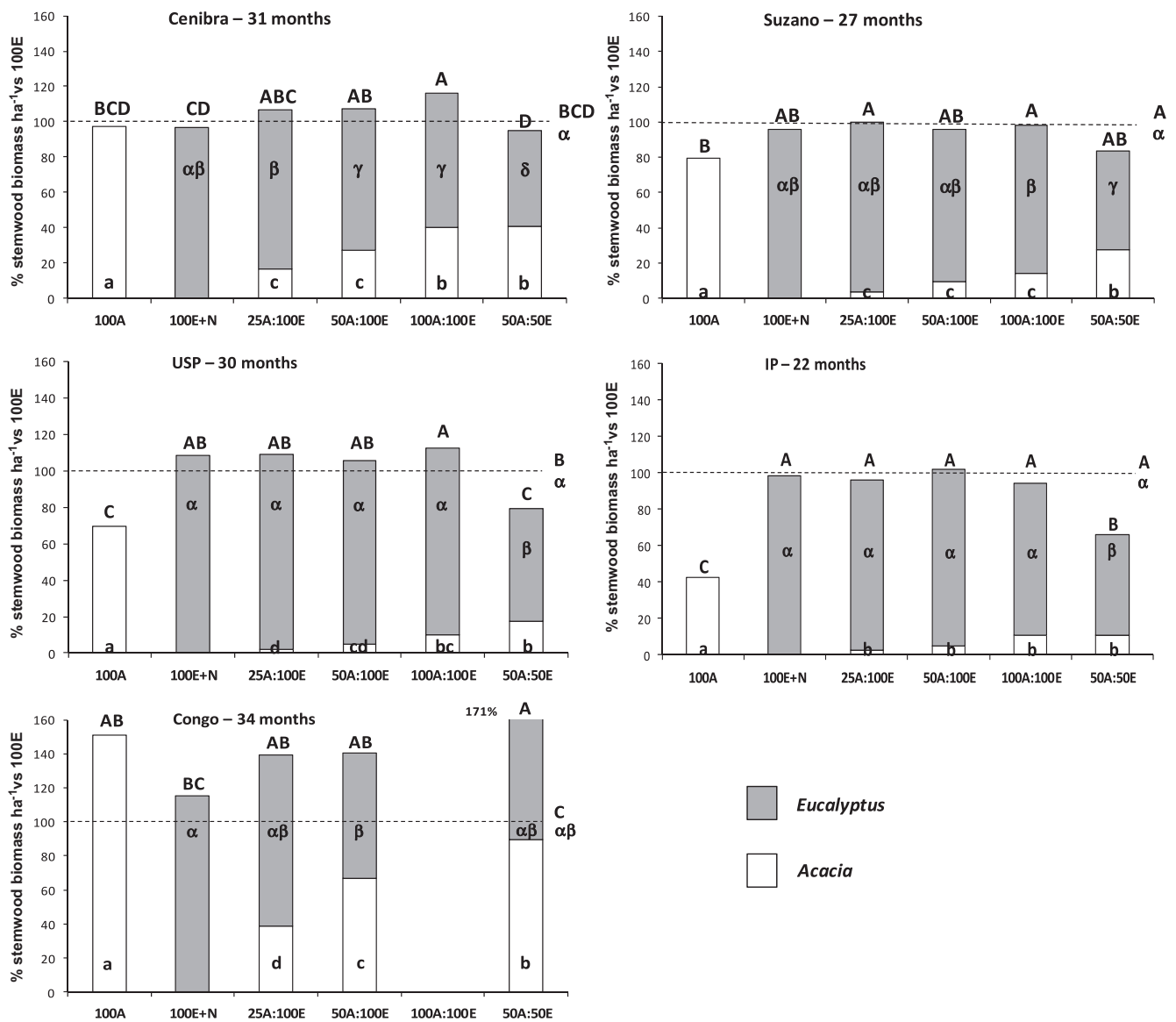


Fig. 4. Time course of mean *A. mangium* circumference over stand rotation depending on sites. Significant differences between at least two treatments are indicated by \* ( $P < 0.05$ ) and \*\*\* ( $P < 0.001$ ). Different letters indicate significant differences between treatments ( $P < 0.05$ ) at the last date of measurement.

than in Cenibra. However, no depressive effect due to *A. mangium* was observed on *Eucalyptus* tree growth in Congo in 50A:50E and 25A:100E, and only a 21% reduction was found in *Eucalyptus* production in 50A:100E compared to 100E. *A. mangium* is a species originating from north-eastern Australia, Papua New Guinea and eastern Indonesia, adapted to warm climates with high air moisture (Krisnawati et al., 2011). The climates in Cenibra (air temperature) and Congo (air temperature + humidity) were more suitable for *A. mangium* growth than at the other sites. *E. grandis* is a highly productive *Eucalyptus* species native to Queensland and New South Wales in Australia. It is well adapted to areas with moderate temperatures (about 20 °C) and 1000–1750 mm year<sup>-1</sup> summer rainfall maximum areas (Florence, 1996; FAO, 1999), as found in USP and Suzano. The hybrid *E. urophylla* × *E. grandis* has been developed worldwide to combine the qualities of *E. grandis* and those of *E. urophylla*. The latter is a native species of Indonesia and Timor, adapted to more tropical conditions in areas where the dry season lasts for several months (FAO, 2001), as found in Cenibra and IP. This hybrid is not fully adapted to very warm and humid climates,

particularly owing to leaf diseases (Hardiyanto and Tridasa, 2000). In the absence of facilitation and/or complementarity between the two species, the following patterns of inter-specific competition for light and soil resources are to be expected: (1) strong competition between *Eucalyptus* trees and *A. mangium* trees at all the Brazilian sites, though less marked in Congo; (2) greater competition between *A. mangium* trees and *Eucalyptus* trees in Congo and Cenibra than in Suzano, USP and IP. The net influences of *Eucalyptus* on *A. mangium* that we observed in our network were consistent with this pattern.

The balance between competitive and facilitative processes changed over time and in relation to site characteristics, which is consistent with our hypothesis. In Brazil, there was little competition between *Eucalyptus* and *Acacia* trees during the first few years after planting. Simulations using the MAESTRA model of leaf area index (LAI) and Absorbed Photosynthetically Active Radiation (APAR) over stand rotation showed in USP higher stand light capture in the mixtures than in mono-specific stands owing to stratified canopies (Le Maire et al., 2012). The model that was both

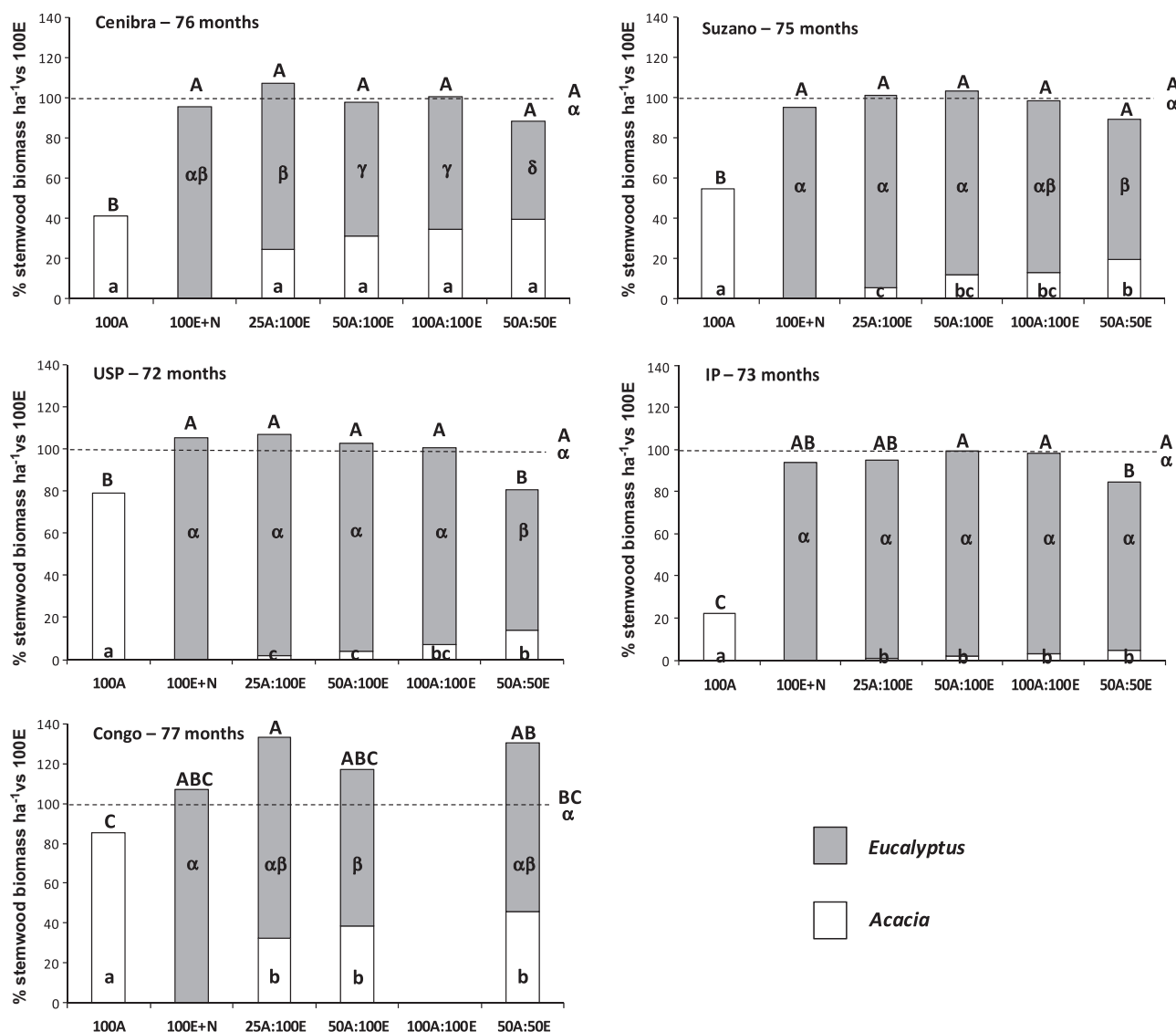


**Fig. 5.** Percentage of stand stemwood at the beginning of stand rotation in comparison to 100E depending on sites. Different letters indicate significant differences between treatments ( $P < 0.05$ ): a, b, etc. for *A. mangium* stemwood;  $\alpha$ ,  $\beta$ , etc. for *Eucalyptus* stem biomass; A, B, etc. for total stemwood biomass. Mean stemwood increment of 100E at the beginning at age 22–34 months of stand rotation was 16.8, 17.8, 11.5, 8.7, and 4.6  $\text{Mg ha}^{-1} \text{year}^{-1}$  in Cenibra, Suzano, USP, International Paper (IP) and Congo sites, respectively. Dashed lines represent 100E treatment.

parameterized and validated at the USP site simulated a higher LAI and APAR in mixture than in 100E from 24 months onwards. This result was consistent with the tendency of higher stand production in nA:100E treatments, except at the IP site where adverse conditions (e.g. low air humidity and a marked dry season in a sandy soil) led to poor *Acacia* growth. However, the increase in LAI and APAR did not lead to greater stemwood biomass at the end of the rotation. Cumulated actual evapotranspiration (AET) almost matched annual rainfall over a rotation of *E. grandis* monoculture in USP (Nouvellon et al., 2011). According to these authors, the AET of *Eucalyptus* plantations in South-East Brazil is lower than rainfall during initial stand growth (up to 1.5–2 years after planting), greater than rainfall during the phase with the highest current annual increment where significant amounts of water are taken up in very deep soil layers ( $\approx 1.5$ –3 years, Christina et al., 2011), and of the same order of magnitude as rainfall at the end of the rotation when no more water may be taken up from deep soil layers. Increasing the stocking density in the additive series by associating acacia trees might have led to a greater use of water stored in deep

soil layers in the first years after planting than was the case for 100E. Therefore, these stands were probably affected by a water shortage sooner than 100E and 100A. Thus, the gain in stand production in the early stages was largely lost by the end of the rotation, probably because of intra- and inter-specific competition for water. Stand production was lower for the 50A:50E treatment than the *Eucalyptus* monocultures and additive treatments at all the Brazilian sites. The high eucalypt growth due to the larger crown (Le Maire et al., 2012) and low intra-specific *Eucalyptus* competition did not compensate for the low *Acacia* production in USP, Suzano and IP, and for the marked inter-specific competition in Cenibra.

In contrast, complementarity between *Acacia* and *Eucalyptus* occurred in Congo over the entire rotation. At this site, deep drainage occurs each year in pure eucalypt stands due to a lower soil retention capacity and lower AET, which is largely the result of lower LAI, net radiation, and atmospheric water demand (lower VPD and wind speed) compared to the Brazilian sites (Nouvellon et al., 2011). Therefore, competition for water between *Eucalyptus* and *Acacia* was probably lower than at the Brazilian sites. This



**Fig. 6.** Percentage of stand stemwood at the end of stand rotation in comparison to 100E depending on sites. Different letters indicate significant differences between treatments ( $P < 0.05$ ): a, b, etc. for *A. mangium* stemwood;  $\alpha$ ,  $\beta$ , etc. for *Eucalyptus* stemwood biomass; A, B, etc. for total stemwood. Mean stemwood increment of 100E at the end harvesting age at 72–77 months of stand rotation was 20.8, 21.1, 18.2, 20.6, and 7.6  $\text{Mg ha}^{-1} \text{ year}^{-1}$  in Cenibra, Suzano, USP, International Paper (IP) and Congo sites, respectively. Dashed lines represent 100E treatment.

competition could also be lowered by potential differences between the two species in terms of soil exploration (Laclau et al., 2012) and/or in seasonal patterns of water and nutrient uptake. Mean *Eucalyptus* stemwood biomass per tree was 68% higher in 50A:50E (400 eucalypts  $\text{ha}^{-1}$ ) than in 100E (800 eucalypts  $\text{ha}^{-1}$ ), at 77 months of age. These figures may be compared to the individual stem volume that was only 37% higher at 400 eucalypts  $\text{ha}^{-1}$  than at 800 eucalypts  $\text{ha}^{-1}$  at 63 months of age in a spacing trial located 10 km away in the same ecological conditions (unpublished data). The high eucalypt biomass production in 50A:50E in comparison with the same eucalypt density in the other trial suggests that competition from neighbouring acacias on eucalypts was likely to be very low. Moreover, the individual above-ground biomass of acacias in 50A:50E was 74% and 127% of that of eucalypts in 50A:50E and 100E, respectively. This noteworthy production might be compatible with the low competition between *Acacia* and *Eucalyptus* trees as a result of an improvement in water use efficiency for the two species, as shown in Australian mixed-species *Eucalyptus* plantations (Forrester et al., 2010) and/or a niche effect enhancing the uptake of water resources for both species. The

partial exclusion of *Acacia* roots from the topsoil layer caused by *Eucalyptus* might occur as observed in mixtures at the USP site (Silva et al., 2009; Laclau et al., 2012). However, this vertical segregation did not lead to transgressive stemwood overyielding (Pretzsch and Schütze, 2009) in USP, which is probably due to the limited water at this site (Laclau et al., 2012).

In addition to species complementarity, facilitation of *A. mangium* on *Eucalyptus* through  $\text{N}_2$  fixation and N transfer was also highly likely in Congo. A 7% higher stemwood biomass was found in 100E + N compared to 100E at the end of the rotation despite an N-fertiliser application at planting in the two treatments, which suggests that soil N deficiency reduced eucalypt growth. An increase in N-fertiliser demand over successive stand rotations of *Eucalyptus* monocultures was shown at this site as a result of a strong unbalance in the N budget (Bouillet et al., 2004; Laclau et al., 2010a). The good climatic conditions at the Congo site for *A. mangium* growth on N-depleted soils favoured  $\text{N}_2$  fixation: 90% of *Acacia* N content was derived from  $\text{N}_2$  fixation in 50A:100E, leading to 340  $\text{kg N ha}^{-1}$  fixed over the first 34 months after planting (Bouillet et al., 2010). Inter-specific facilitation through  $\text{N}_2$

**Table 3**

Mean biomass of harvest residues (leaves + bark + living branches + dead branches) at clear cutting depending on sites ( $\text{Mg ha}^{-1}$ ). Different letters indicate significant differences between treatments ( $P < 0.05$ ): a, b, etc. for *A. mangium* (Ac.) residues; a', b', etc. for *Eucalyptus* (Euc.) residues; A, B, etc. for total plot residues.

Site	100A			100E			100E + N			25A:100E			50A:100E			100A:100E			50A:50E			
	Ac.	Euc.	Total	Ac.	Euc.	Total	Ac.	Euc.	Total	Ac.	Euc.	Total	Ac.	Euc.	Total	Ac.	Euc.	Total	Ac.	Euc.	Total	
Cenibra (76 months)	22.8	21.6	20.9	13.6	18.3	31.9	18.6	15.3	33.9	22.5	15.4	37.9	22.1	11.3	33.4							
	a	a'	a'b'	a	b'	ABC	a	c'	A	a	c'	A	a	d'	AB							
Suzano (75 months)	51.9	41.2	39.5	5.8	39.3	45.1	13.4	37.5	50.9	15.2	35.1	50.4	17.0	56.0	73.0							
	a	b'	b'	c	b'	BCD	bc	b'	BC	b	b'	BC	b	a'	A							
USP (72 months)	45.7	27.2	28.6	1.7	28.5	30.2	3.8	26.7	30.5	6.6	25.3	31.9	9.2	27.0	36.2							
	a	a'	a'	c	a'	C	bc	a'	B	bc	a'	BC	b	a'	B							
Int. Paper (73 months)	15.2	26.7	25.1	1.3	25.1	26.3	2.9	26.0	28.9	5.4	25.4	30.8	4.4	22.4	26.9							
	a	a'	a'b'	b	a'b'	AB	b	a'	AB	b	a'	A	b	a'	AB							
Congo (77 months)	30.0	14.9	14.5	10.4	13.0	23.4	13.4	11.2	24.6	–	–	–	15.6	12.7	28.3							
	a	a'	a'	b	a'	B	b	a'	AB				b	a'	AB							

fixation might also occur in Brazil during the first years after planting. In *Eucalyptus* monocultures, an early response to N fertilisation is commonly observed in South-East Brazil (Gonçalves et al., 2008; Laclau et al., 2010a).  $\text{N}_2$  fixation was estimated at  $31 \text{ kg N ha}^{-1}$  for the first 30 months after planting in 50A:100E in the USP experiment (Bouillet et al., 2008). However, this possible facilitation was not observed over the entire stand rotation: the initial gain in stem volume in pure *Eucalyptus* stands resulting from N fertilisation is largely lost at the end of the rotation (Gonçalves et al., 2008) due to other limiting factors, mostly water shortage.

Few studies focused on the spatial and temporal changes between facilitative and competitive processes in mixed-species plantations of *Eucalyptus* and NFS. This balance shifted in relation to soil fertility in mixtures of *Eucalyptus saligna* and *Falcataria molucana* in Hawaii (Boyden et al., 2005). On N-deficient soils, *Eucalyptus* increased *Falcataria* growth by degrading recalcitrant soil carbon pools and increasing P availability for *Falcataria* trees. In contrast, high *Eucalyptus* growth on N-rich soils led to high P uptake by eucalypts and to a decrease in P availability for *Falcataria* trees. A facilitative influence of *Falcataria* on *Eucalyptus* trees was also observed with an increase in soil P availability, probably as a result of higher rates of  $\text{N}_2$  fixation in P-rich soils. In Australia, the facilitative effect of *Acacia mearnsii* on *Eucalyptus globulus* was found to decrease as the productivity of pure *E. globulus* stands increased (Forrester et al., 2011). It was also observed that the growth advantage associated with being in a mixture increased over time for *E. globulus*. In mixtures this species benefitted from enhanced N and P availability due to  $\text{N}_2$  fixation by *A. mearnsii*, higher rates of nutrient cycling, and reduced light competition from 6 years onwards as *E. globulus* overtopped *A. mearnsii*. Our results are consistent with these studies. The balance between facilitative and competitive processes in the mixtures was more favourable in Congo where the soils are deficient in N but not in P (Bouillet et al., 2004; Laclau et al., 2010a), and where *Eucalyptus* productivity is low than in Brazil where high stand production is mainly limited by water resources.

#### 4.2. Prospects

Mixed-species plantations of *Eucalyptus* with *A. mangium* might be a valuable alternative to *Eucalyptus* monocultures. A marked

increase in stand production is unlikely in areas such as South-Eastern Brazil where *Eucalyptus* monocultures are highly productive and almost all the rainfall is lost to evapotranspiration. However, the introduction of  $\text{N}_2$ -fixing trees, such as *A. mangium*, could contribute to improving the nutrient N budget that is commonly unbalanced in *Eucalyptus* plantations (Du Toit, 2003; Corbeels et al., 2005; Laclau et al., 2010a), and to reducing the needs of N fertilisers. The larger amounts of harvest residues left at the soil surface and the greater litter fall in mixtures compared to mono-specific stands (Nouvellon et al., 2012) might also enhance soil C sequestration in the long term (Kaye et al., 2000; Resh et al., 2002). However, C and N contents in the mineral soil were not higher in 50A:50E at the end of the rotation in USP despite the fact that soil N mineralisation rates were twice as high in 100A than in 100E (Voigtlaender et al., 2012) and we still have no information on the potential change in organic matter quality when associating *A. mangium* to *Eucalyptus* (Kaye et al., 2000). Soil N mineralisation in 50A:50E was intermediate between 100A and 100E at the four Brazilian sites (data not shown).

An extension of *Eucalyptus* plantations is expected worldwide and, particularly, in Brazil where their total area should reach 11–14 million hectares in 2020 (ABRAF, 2011). In Brazil, a high proportion of future plantations are likely to be established in the northern states (e.g. Pará, Tocantins) with high temperatures and air humidity, and rainfall that is well distributed throughout the year. *Eucalyptus* plantations are less productive in Amazonia than in South-Eastern Brazil (de Souza et al., 2004; Demolinari et al., 2007; Behling et al., 2011) and well-adapted genotypes have yet to be created (Alfenas et al., 2011; Gonçalves et al., 2012). In contrast, the climatic conditions are very favourable for *A. mangium* growth (de Souza et al., 2004). Thus, given that water is not a limiting factor, the association of *A. mangium* with *Eucalyptus* could lead to a significant increase in productivity as found in Congo. As high rainfall increases the risk of nutrient loss via leaching or run-off,  $\text{N}_2$  fixation should be particularly important for balancing the soil N budgets. The greater amounts of harvest residues in mixtures should also help maintain stand productivity in highly-weathered sandy soils, where a large proportion of soil fertility comes from organic matter above the mineral soil (Laclau et al., 2010b). Moreover, a faster closure of the stand canopy compared to monocultures might reduce weeding costs and the risks of poor

stand growth due to strong weed competition (Behling et al., 2011).

Specific silvicultural practices have to be designed for mixed-species plantations of *Eucalyptus* and NFS. Although *A. mangium* was only sensitive to strong winds in 100A owing to the development of large crowns, it would be better not to plant mixtures with this species in windy areas. The risk of trees being blown over could also be lowered by singling multi-stem trees in the early stages of stand development (Krisnawati et al., 2011). Adapted spacing and spatial arrangements (e.g. species in lines) would have to be found to obtain maximum stand production and facilitate harvesting operations.

Here, we have shown the potential of mixed-species plantations of *E. grandis* (or *E. urophylla* × *grandis*) and *A. mangium* in various ecological conditions. Our results suggest that compared to eucalypt monocultures, these associations are likely to enhance above-ground stand production in warm humid tropical conditions, on poor nutrient soils with low water constraints. Mixtures might also help achieve sustainable yields through N<sub>2</sub> fixation and high N and C cycling. Additional research is required to further our understanding of the ecological mechanisms that drive the competitive and facilitative processes between species as a function of the ecological conditions and silvicultural practices. Special attention should also be given to the environmental impacts of silviculture (with water and nutrient budgets in the soil) in mixed-species plantations and the vulnerability of such ecosystems to climate changes. The diversification of NFS adapted to mixtures should also be developed, particularly with native species (Coelho et al., 2007). Research programmes should be conducted as part of a large international network in order to obtain a general overview of the potential of mixed-species plantations of *Eucalyptus* and NFS in tropical regions.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.09.019>.

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