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Production and carbon allocation in monocultures and mixed-species plantations of *Eucalyptus grandis* and *Acacia mangium* in Brazil

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Introducing nitrogen-fixing tree species in fast-growing eucalypt plantations has the potential to improve soil nitrogen availability compared with eucalypt monocultures. Whether or not the changes in soil nutrient status and stand structure will lead to mixtures that out-yield monocultures depends on the balance between positive interactions and the negative effects of interspecific competition, and on their effect on carbon (C) uptake and partitioning. We used a C budget approach to quantify growth, C uptake and C partitioning in monocultures of *Eucalyptus grandis* (W. Hill ex Maiden) and *Acacia mangium* (Willd.) (treatments E100 and A100, respectively), and in a mixture at the same stocking density with the two species at a proportion of 1 : 1 (treatment MS). Allometric relationships established over the whole rotation, and measurements of soil CO_2 efflux and aboveground litterfall for ages 4–6 years after planting were used to estimate aboveground net primary production (ANPP), total belowground carbon flux (TBCF) and gross primary production (GPP). We tested the hypotheses that (i) species differences for wood production between *E. grandis* and *A. mangium* monocultures were partly explained by different C partitioning strategies, and (ii) the observed lower wood production in the mixture compared with eucalypt monoculture was mostly explained by a lower partitioning aboveground. At the end of the rotation, total aboveground biomass was lowest in A100 (10.5 kg DM m^{-2}), intermediate in MS (12.2 kg DM m^{-2}) and highest in E100 (13.9 kg DM m^{-2}). The results did not support our first hypothesis of contrasting C partitioning strategies between *E. grandis* and *A. mangium* monocultures: the 21% lower growth (ΔB_w) in A100 compared with E100 was almost entirely explained by a 23% lower GPP, with little or no species difference in ratios such as TBCF/GPP, ANPP/TBCF, ΔB_w/ANPP and ΔB_w/GPP. In contrast, the 28% lower ΔB_w in MS than in E100 was explained both by a 15% lower GPP and by a 15% lower fraction of GPP allocated to wood growth, thus partially supporting our second hypothesis: mixing the two species led to shifts in C allocations from above- to belowground, and from growth to litter production, for both species.

Keywords: carbon partitioning, fast-growing plantations, gross and net primary productivity, interspecific interactions, N$_2$ fixing tree species, soil CO_2 efflux

Introduction

The contribution of tree plantations to world wood supplies has increased sharply over recent decades (FAO 2009). In the tropics, several fast-growing *Eucalyptus* species are widely planted, especially in Brazil where eucalypt plantations cover 4.5 million ha (ABRAF 2010). They are mainly managed for pulpwood and charcoal production, and their high productivity (~40 m^3 ha^{-1} $year^{-1}$; ABRAF 2010, Ryan et al. 2010, Le Maire et al. 2011a) leads to high exports of nutrients with wood products, especially nitrogen (N) (Laclau et al. 2010a), thus raising concerns about their sustainability. Although commercial forest companies generally compensate for nutrient exports with nutrient inputs via fertilization, this amounts to a major cost that is likely to increase in the future due to the rising trend of fertilizer prices worldwide (Cordell et al. 2009). This concern may be partly addressed by introducing nitrogen (N_2)-fixing species in eucalypt plantations (Kelty 2006, Forrester et al. 2006a). Carefully chosen combinations of species have the potential to improve N and phosphorus (P) cycling, wood production, soil fertility and carbon (C) sequestration (Richards et al. 2010), compared with *Eucalyptus* monocultures. N_2-fixing species of the genus *Acacia* have been proposed for such mixtures, including *Acacia mangium*, one of the most widely planted species in tropical Asia (Konda et al. 2010, Inagaki et al. 2010).

Whether or not a mixture will out-yield monocultures depends on the balance between positive interactions (competitive reduction or facilitation; Forrester et al. 2006a), and negative effects of interspecific competition. Differences in resource requirements between the two species may lead to competitive reduction. N_2 fixation by *Acacia* trees (Bouillet et al. 2008) can improve mineral N availability in the soil (Binkley et al. 1992, Forrester et al. 2005a, Voigtlaender et al. 2012) and facilitate *Eucalyptus* growth. Stratification of the canopies of the two species (Binkley 1992, Bauhus et al. 2004, Hunt et al. 2006, Laclau et al. 2008), or improved exploration of the soil by their root systems (Jose et al. 2006), may also increase the capture of light, water and nutrients (Kelty 2006). Although some of these aspects have been studied, little is known about C allocation in these mixed-species (MS) plantations (Forrester et al. 2006a). Are differences in wood production between MS plantations and monocultures mostly explained by differences in gross primary productivity (GPP), or by shifts in the fraction of GPP used for aboveground wood production? How is the C allocation pattern of each species in the mixture influenced by above- and belowground interactions between species?

Studies on C allocation in forest ecosystems have often considered five sinks (Ryan et al. 2004, 2010, Litton et al. 2007): total belowground C flux (TBCF), corresponding to the amount of C used for root production, root respiration and exudation, and to sustain root symbionts (e.g., N_2-fixing bacteria and mycorrhizae); leaf production (P_l), and respiration (R_l), aboveground woody production (P_w) and respiration (R_w). The processes controlling the allocation of C to these sinks are still poorly understood, thus limiting the ability of process-based models to accurately simulate C cycling in forest ecosystems (Lacointe 2000, Litton et al. 2007). However, empirical evidence has shown (i) shifts in C allocation with ontogeny (Ryan et al. 2004); (ii) plasticity of C allocation with resource availability, with, as a general trend, increased partitioning to the plant component that forages for the most limiting resource (partitioning is defined here according to the terminology of Litton et al. (2007), as the flux of C to a particular component, as a fraction of GPP). For instance, fertilization generally shifts partitioning from belowground to aboveground, by alleviating soil nutrient limitations, thus contributing to increased wood production (Haynes and Gower 1995, Keith et al. 1997, Giardina et al. 2003, Litton et al. 2007, Ryan et al. 2010). Nutrient availability may also affect C allocation through changes in leaf and/or fine root longevity (Richards et al. 2010); for instance, K fertilization has been found to shift C partitioning from below- to aboveground in eucalypt plantations (Epron et al. 2012), but also to decrease partitioning to leaf production, despite much higher leaf biomass, due to its strong positive effect on leaf longevity, responsible for the increase in leaf biomass (Laclau et al. 2009, Epron et al. 2012, this issue).

All these factors known to affect C partitioning (ontogeny and resource availability) are likely to be altered in MS plantations, compared with monocultures: mixtures generally change the ontogenetic development of individual species (Richards et al. 2010); canopy stratification and nutritional interactions affect the amount of resources available to each species. Shifts in C partitioning for individual species are therefore likely and they will determine the stand-scale C partitioning of the mixture. In MS plantations, shifts in C might also be mediated (i) by changes in the soil microbial communities (Fan et al. 2008); (ii) by sophisticated interactions between the root systems of the two neighbouring species, which may enhance root growth and belowground C allocations for either or both species (de Kroon 2007); (iii) by changes in the canopy structure (e.g., stratification), which not only affects the light environment of each species, but also their exposure to wind forces and resulting bending stress, which are known to influence plant allometry and C allocation (Meng et al. 2006, Coutand et al. 2008, Coutand 2010).

Surprisingly, there have been very few studies comparing C allocation patterns in mixtures and monocultures. To our knowledge, Forrester et al. (2006b) was the only study that compared C allocation patterns in single- and mixed-species plantations including a N_2-fixing species. In this study, the aboveground biomass and wood production in 11-year-old mixtures of *Eucalyptus globulus* (Labill.) and *Acacia mearnsii* (De Wild.) was much higher than in monocultures of the same

species. The better performance of the mixtures compared with monocultures was explained by higher overall (above- and belowground) productivity, and greater partitioning aboveground. According to Forrester et al. (2006b), this shift in C partitioning may have resulted from increases in the availability of N and P in the mixtures compared with monocultures (Forrester et al. 2004). Their results were therefore consistent with the global trends observed for C allocation in forest ecosystems: conditions that favour high productivity (GPP or NPP) increase partitioning to aboveground wood production, and decrease partitioning to TBCF (Litton et al. 2007). Does the reverse hold? Mixed-species plantations do not always outperform monocultures (Forrester et al 2005b, Kelty, 2006). When species combinations lead to mixtures that are less productive than monocultures, is the lower wood production in the mixture partially explained by lower C partitioning aboveground, and greater partitioning to TBCF?

To tackle this question, C allocations were investigated in monoculture stands of *Eucalyptus grandis* (W. Hill ex Maiden) and *Acacia mangium* (Willd.) and mixtures of these species in a proportion of 1 : 1 (50A : 50E), in southeastern Brazil. Tree growth and litterfall were measured over a 6-year rotation, and a mass balance approach (Ryan et al. 2010) was used to estimate TBCF and C allocations over the last 2 years before harvesting. Unlike the stands examined by Forrester et al. (2006b), the mixtures in our study produced less wood than *E. grandis* monocultures (Laclau et al. 2008). We put forward the hypothesis that (i) species differences for wood production between *E. grandis* and *A. mangium* monocultures were partly explained by different C partitioning strategies, and (ii) the lower wood production in the mixture compared with eucalypt monoculture was mostly explained by lower partitioning aboveground.

Materials and methods

Study site and experimental design

The study was carried out at the Itatinga Experimental Station (University of São Paulo) located at a latitude of 23°02′S and a longitude of 48°38′W. The soils at the experimental site (860 m above sea level; slope <3%) are Ferralsols according to the FAO classification, developed on Cretaceous sandstone, Marília formation, Bauru group. These deep soils (Christina et al. 2011) are characterized by high textural uniformity below a depth of 1 m (clay content around 13% in the A1 horizon and ranging from 20 to 25% between 1 and 6 m in depth). The effective cation exchange capacity ranges from 2 to 20 $mmol_c$ kg^{-1} in the upper 3 m of soil and the amounts of exchangeable 'bases' are <2 $mmol_c$ kg^{-1} below a depth of 5 cm (Voigtlaender et al. 2012).

The mean annual rainfall from May 2003 to April 2009 (period covered by the 6-year rotation) was 1280 mm, with a cold season from June to September. The average annual temperature was 21.3 °C, with an absolute minimum of 4.0 °C recorded in June 2007 (Figure 1).

The experiment was set up in a former *Eucalyptus saligna* Sm. plantation managed as a coppice without fertilizer application from 1940 to 1998, followed by an *E. grandis* rotation (1998–December 2002). A complete randomized block design was established in May 2003 with seven treatments and four blocks, in order to assess the influence of *A. mangium* trees on the growth of *E. grandis* seedlings (half-sib family from the Suzano Company, Sao Paulo, SP, Brazil). Each plot was 30 m × 30 m in size, with an inner plot of 18 m × 18 m and two buffer rows (see Laclau et al. (2008) for a complete description of the experimental layout). Our study was carried out in three treatments and three blocks, planted at a stand density of 1111 trees ha^{-1} (3 m × 3 m spacing) without N fertilization: the *A. mangium* and *E. grandis* monoculture stands (A100 and E100, respectively), and the mixture (50A : 50E, MS hereafter) in a proportion of 1 : 1 (555 trees per hectare of each species, planted alternately in the row, and between adjacent rows).

Seedlings were planted between the rows of the previous plantation after soil tillage with a ripping tine to a depth of 40 cm. *Acacia mangium* seedlings were inoculated with *Rhizobium* strains selected by EMBRAPA for their N$_2$ fixation capacities and they exhibited high levels of nodulation in the nursery. Two tons per hectare of dolomitic limestone was applied, along with 40 g P, 9 g K, 3 g B, 6 g Fe, 3 g Zn and 1 g Mn for each tree at the time of planting. In addition, 25 kg K ha^{-1} was applied at 6, 12 and 18 months after planting. Further details about site preparation and fertilization can be found in Laclau et al. (2008) and Voigtlaender et al. (2012).

Tree growth, litterfall and aboveground net primary production

From planting (May 2003) to the end of the rotation (clear-cut in April 2009), tree height (*H*, m) and circumference at breast height (*C*, m) were measured every 6 months on the 36 central trees of each plot (excluding the two buffer rows). Crown diameter was measured for each tree in two perpendicular directions and used to estimate the crown area (A_c, m^2). Most of the acacias were multi-stem trees and the circumference of all the stems with a diameter at breast height (DBH) exceeding 2 cm was measured on each inventory. For multi-stem trees, the cross-sectional area at breast height of all the stems was cumulated for each tree and an 'equivalent diameter' was calculated from the total cross-sectional area of the tree.

The biomass of aboveground components, i.e., stemwood, stembark, living branches, dead branches and leaves, was estimated annually from inventories. Species-specific allometric equations were established in all treatments from destructive samplings of 10 trees of each species over the range of cross-sectional areas, at 30, 54 and 72 months after planting. At 12
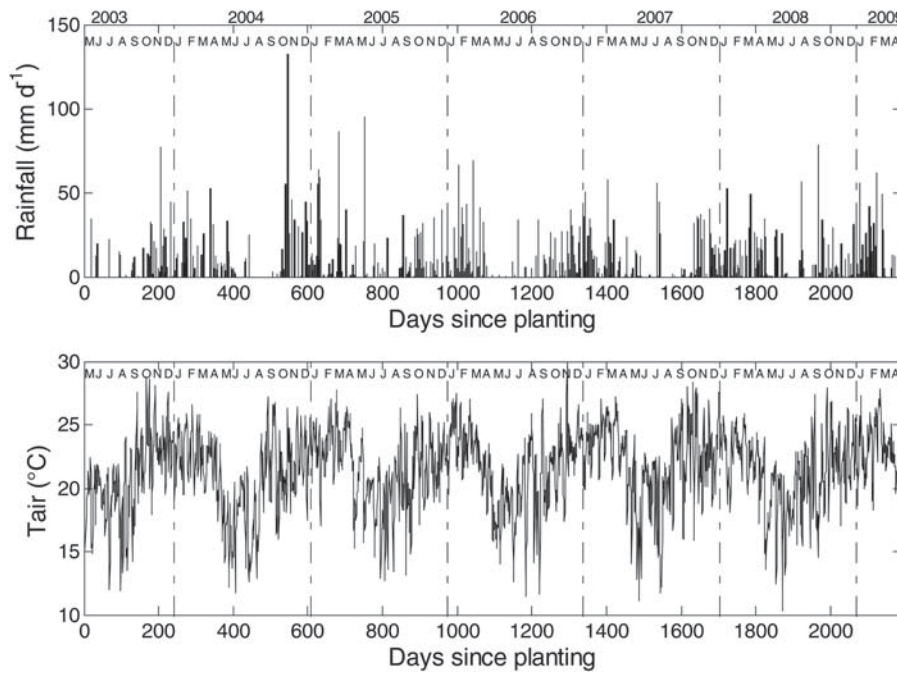
Figure 1. (a) Daily rainfall (mm day^{-1}), (b) daily mean air temperature (°C) recorded at the Itatinga experimental site (rainfall) and at Botucatu (~40 km from Itatinga; air temperature) over the 6 years of the rotation (May 2003–April 2009).

and 18 months of age, six and eight trees were sampled in each monoculture treatment, respectively. The trees were felled, measured for total height and for height at green crown base, and the dry mass of their components was measured as described in Laclau et al. (2008). Carbon and N concentrations were determined in samples of each component for each tree (Laclau et al. 2008). The dry weight of each component j of tree i, $B_{i,j}$, was computed as

$$B_{i,j} = c_j + b_j X_i^{d_j} + \varepsilon_{i,j} \qquad (1)$$

where X_i is the independent variable (generally DBH$^2 \times$ H, or either A_c, H, DBH, $A_c \times$ H); c_j, b_j, and d_j are the parameters to be estimated and $\varepsilon_{i,j}$ the residuals not explained by the models (Laclau et al. 2008). Observations were assumed to be uncorrelated: trees in the same stand were cut as far as possible from each other and thus reduced the potential competition between them. Equation (1) was fitted for each age, treatment and species using the linear and nonlinear regression procedures of SAS software (REG and NLIN, respectively; see Laclau et al. 2008 for more details about the fitting steps and procedure). The allometric relationships (see Tables S1 and S2 available as Supplementary Data at Tree Physiology Online) were then applied to the plot inventories at each age (within 6 months after or before the corresponding destructive sampling) to estimate the biomass of each component at plot level.

Litterfall was collected every 28 days over the whole rotation in treatments 100E and 100A, and over the last 2 years (January 2007–April 2009) in the MS treatment. Leaf and fruit litterfall was collected in five traps (52 cm × 52 cm) per plot installed at various distances from the trees in the 100A and 100E treatments and in 10 traps per plot in the MS treatment (replicated in three blocks). Dead branches and bark were collected in an area of 9 m^2 delimited between four trees in each plot (replicated in three blocks for the three treatments). Litter was separated by species and component of the litter, and then dried at 65 °C for 72 h before weighing. The replicates in the three blocks were mixed into one sample of each component of litterfall for each 28-day period and ground for chemical analysis (including C content).

Aboveground net primary production (ANPP) was computed for each year, as the sum of annual biomass increments of all aboveground tree components, and annual litterfall (herbivory was considered negligible). Similarly, annual leaf production, P_l, and aboveground woody production, P_w (ANPP $= P_l + P_w$), were computed as the sum of annual leaf litterfall, L_l, and annual changes in leaf biomass, ΔB_l, and as the sum of annual increments of woody biomass (stem wood, stem bark, living and dead branches), ΔB_w, and woody litterfall, L_w, respectively. In the MS treatment, ANPP, P_w and P_l were quantified for each species and for the stand. ANPP, P_w and P_l were expressed either in kg DM m^{-2} year^{-1} or in kg C m^{-2} year^{-1}. Production values in kg C m^{-2} year^{-1} were calculated using the measured C content of each component (values ranging from 0.46 g C g DM^{-1} in medium-sized roots and wood to 0.50 g C g DM^{-1} in leaves for eucalypt, and from 0.45 g C g DM^{-1} in bark to 0.50 g C g DM^{-1} in leaves for acacias; data not shown).

Total belowground C allocation

Total belowground carbon flux (TBCF, kg C m^{-2} year^{-1}) was estimated for the last 2 years of the rotation (May 2007–April 2009) using a mass balance approach (Giardina and Ryan 2002, Ryan et al. 2010):

$$ TBCF = F_{SCUM} + F_{ECUM} - L_{CUM} + \frac{\Delta(B_R + C_L + C_S + C_T)}{\Delta t} \quad (2) $$

where F_{SCUM} (kg C m^{-2} year^{-1}) is the cumulative annual soil CO_2 efflux (averaged over time interval $\Delta t = 2$ years), F_{ECUM} (kg C m^{-2} year^{-1}) is the annual amount of C exported through leaching (dissolved organic C) or erosion, L_{CUM} is the annual litterfall (kg C m^{-2} year^{-1}), B_R is C in root biomass, C_L is the forest floor C, C_S is the C in the mineral soil and C_T is the C in decomposing stumps and roots from the prior plantation.

Soil CO_2 effluxes (F_s) were measured every 2 weeks from January 2007 to April 2009 using a dynamic closed-path Li8100 system equipped with a 20 cm diameter Li8100-103 respiration chamber (LiCor Inc., Lincoln, NE, USA). Nine PVC collars were installed in each monoculture plot, using the sampling scheme shown in Figure 2. However, in contrast to what is shown in Figure 2, the collars corresponding to the nine positions were not gathered (they were distributed close to nine different trees). In each plot of the MS treatment, 18 collars were installed (9 positions × 2 species) around 18 different trees. The total number of collars was therefore 108 (9 × 3 × 2 for the six monoculture plots, and 18 × 3 for MS plots). PVC collars were installed 1 month before the beginning of measurements. Soil volumetric water content in the 0–6 cm soil layer (θ_v, m^3 m^{-3}) was measured simultaneously within 5 cm of the collars using a soil moisture probe (Theta Probe ML2X, Delta-T Device Ltd, Cambridge, UK). Cumulative soil CO_2 efflux was estimated for each PVC collar using linear interpolations of F_S between measurement dates over the 2-year measurement period.

L_{CUM} was obtained by summing monthly litterfall measurements. F_{ECUM} was considered negligible, as in most studies (e.g., Forrester et al. 2006b, Ryan et al. 2010), since erosion was not observed at this site, and deep fluxes of DOC are negligible (Maquère 2008).

The forest floor C was measured at ages 48 months and 72 months (end of the rotation) in order to estimate ΔC_L. The same sampling scheme as for soil CO_2 efflux measurements (Figure 2) was used. The forest floor was sampled with a 15 cm radius circular frame at each position and divided into three components: Oi (non-fragmented material), Oe (coarse fragments) and Oa (finely fragmented material). The nine samples per component collected in each plot were manually homogenized and one composite sample per plot in monoculture stands (two composite samples per plot in MS, one close
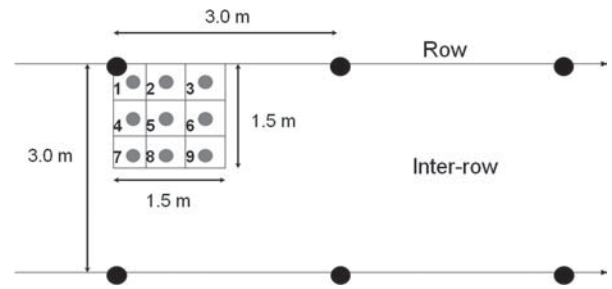

Figure 2. Sampling grid scheme for soil respiration measurements indicating the nine positions (grey-filled circles) where the PVC collars were placed. The nine positions were not gathered close to a single tree (black-filled circles), but distributed close to nine different trees in each single-species plot, and around 18 different trees in each MS plot (9 positions × 2 species). The total number of collars was 108 (nine positions × 3 blocks × 2 treatments for the two single-species treatments, and nine positions × 2 species × 3 blocks for the MS treatment).

to each tree species) was ground to pass through a 2 mm mesh stainless-steel screen. The ash content of the forest floor samples was determined by combustion for 4 h at 450 °C. Dry weight values for the forest floor samples were then corrected to eliminate the effect of remaining soil particles. Carbon and N concentrations in litter were determined by a Carlo Erba CHN 1110 elemental analyser (Milan, Italy). More details about these measurements, as well as the mean concentrations of total C and N in the components of the forest floor for the three treatments at age 72 months, can be found in Voigtlaender et al. (2012). C_L was computed from the dry weight and C concentrations of the different forest floor components.

The amount of C released by the decomposition of stumps and roots from the prior rotation (ΔC_T) was estimated in each plot. Stumps were surveyed at the end of our study period, 6 years after planting, by measuring the diameter on the top of the stumps in all the plots. Twenty old stumps, and their coarse roots (diameter >1 cm), were excavated and allometric relationships between stump dry weight and diameter were established and applied to the inventory to estimate stump necromass at the end of the rotation, in April 2009. In an adjacent stand with decomposing stumps of the same eucalypt species, 25 and 10 stumps (plus their coarse roots) were excavated at harvest time and 4.5 years after clear-cutting, respectively, to establish allometric equations at each age. The three equations ($R^2 > 0.85$ for all the equations used) were applied in each plot of our experiment (with a correction for the changes in stump diameter with stump ageing) to estimate stump necromass at the harvest of the previous rotation, as well as at 4.5 and 6 years after planting. These data were used to adjust a model of stump decomposition (exponential decay with adjusted coefficient $k = 0.184$ year^{-1}; $R^2 = 0.96$), which was applied to estimate ΔC_T from age 4 to 6 years after planting in each plot.

Root biomass was measured at several stand ages to estimate ΔC_R. Coarse root biomass was measured at age 72 months for 15 eucalypt trees and 15 acacia trees covering the range of cross-sectional areas in single- and mixed-species stands. All the roots of each tree with a diameter >10 mm were excavated, weighed and a subsample was dried at 65 °C to estimate the total dry weight. Treatment-specific allometric relationships were established for each species and applied to inventories to estimate the coarse root biomass in each plot at ages 48 and 72 months. Medium-sized roots (diameter between 3 and 10 mm) of the two species were excavated from 36 pits (1.5 × 1.5 m in area and a depth ranging between 1 m and 3 m) from 18 to 72 months after planting in single- and mixed-species stands. A relationship between aboveground dry matter and medium-sized root biomass was established for each species and used to estimate medium-sized root biomasses in each plot at 48 and 72 months of age. Fine root biomass (diameter <3 mm) was quantified with a root auger at age 60 months (a total of 108 positions sampled in the 100A, 100E and MS plots down to a depth of 2 m). Fine root biomass was strongly correlated to leaf biomass at the early growth stages (Laclau et al. 2008). Changes in fine root biomass between ages 48 and 72 months were considered negligible as leaf biomass varied little between the two ages and the total biomass of fine roots was low in comparison with the other tree components.

Soil C stocks down to a depth of 15 cm quantified at age 72 months in the same plots were not significantly different between the 100A, 100E and MS treatments (Voigtlaender et al. 2012). Another study (Maquère et al. 2008) showed that plantation management has little influence over soil C stocks in that region. Changes in C stocks in the mineral soil (ΔC_S) were therefore considered negligible for our 2-year study period.

Partitioning of gross primary production

Gross primary production (GPP, kg C m^{-2} year^{-1}) between ages 48 and 72 months was computed as the sum of total aboveground C flux (TACF; kg C m^{-2} year^{-1}), and TBCF. TACF represents the flux of C allocated to ANPP and to aboveground respiration, R_a (respiration of leaves, bark and wood), which was assumed to scale isometrically with ANPP:

$$R_a = ANPP\left(\frac{1 - CUE}{CUE}\right) \qquad (3)$$

where CUE is C use efficiency (Dewar et al. 1998, DeLucia et al. 2007) for aboveground production (CUE = ANPP/TACF). GPP was therefore computed as

$$GPP = \frac{ANPP}{CUE} + TBCF \qquad (4)$$

We used the same CUE value for the two species and the three treatments, 0.53, a value reported for *E. saligna* in Hawaii (Giardina et al. 2003), and also used for nearby *E. grandis* plantations by Epron et al. (2012). The partitioning of GPP to P_l, P_w, R_a and TBCF for the three treatments was then compared (see 'Statistical analyses'). As in some previous studies (Palmroth et al. 2006, Forrester et al. 2006b), treatment comparison of C allocation patterns was also made on the basis of several ratios whose accuracy was independent of our assumed CUE value (see the Discussion section): ANPP/TBCF, B_l/ANPP and B_w/ANPP.

LAI, APAR and LUE

In order to interpret differences in GPP between treatments, the leaf area index (LAI), photosynthetically active radiation absorbed by the canopy (APAR), production efficiency (PE) and light-use efficiency (LUE) were estimated for the last two years of the rotation. LAI was obtained for each species and treatment from allometric relationships (power functions) relating tree leaf area (A_t) to DBH. Destructive measurements of A_t were made on the same trees that were used for destructive sampling of biomass. A_t was estimated for each sampled tree from measurements of the leaf biomass and specific leaf area (SLA) in three crown sections (lower, middle and upper), as described in Nouvellon et al. (2010) and le Maire et al. (2011b). A_t for each tree in the plots and LAI were computed by applying these allometric relationships for A_t to DBH measurements (inventories). Estimated A_t values were also used as inputs into the MAESTRA model (http://www.bio.mq.edu.au/maestra/; Medlyn 2004), together with other measurements (leaf angles, crown sizes, distribution of leaf area within the crowns, coordinate locations of each tree, leaf and soil optical properties, incoming PAR, etc.) to estimate APAR at the tree and stand scales (see le Maire et al. 2012 for more details).

Production efficiency was estimated as the ratio GPP/LAI, and LUE as the ratio GPP/APAR (LUE$_{GPP}$), ANPP/APAR (LUE$_{ANPP}$) and ΔB_w/APAR (LUE$_{\Delta B_w}$).

Statistical analyses

Cumulated soil CO$_2$ effluxes from 48 to 72 months after planting were tested using a three-way analysis of variance (ANOVA) with treatment, block and sampling position as the main factors, and the position × treatment interaction. Two-way ANOVAs were used to test the treatment and block effects for each studied variable (P_l, P_w, ΔB_w, TACF, ANPP, L_{cum}, ΔB_R, ΔC_L ΔC_T, TBCF, GPP, LAI, APAR) as well as for selected ratios between variables. Homogeneity of variances was tested by Levene's test and the normality of residue distribution was checked. Original values were transformed when necessary. The probability level used to determine significance was $P < 0.05$. When significant differences between treatment levels were detected, the Student–Newman–Keuls multiple range test was used to

compare treatment means. All the data were processed using the SAS 9.2 software package (SAS Inc., Cary, NC, USA).

Results

Tree growth

Vertical growth was much faster for the eucalypts than for the acacias, leading to a stratified canopy in the MS stands (Figure 3a). Domination by eucalypts in the MS stands did not increase eucalypt vertical growth, compared with E100, but decreased acacia vertical growth, compared with A100, from age 4 years onwards. The mean tree height in the MS plots (for all the trees of the two species) was intermediate between the two monoculture stands. By contrast, stand basal areas (BAs) were not significantly different in the three treatments (Figure 3b). Eucalypt dominance in the MS stands considerably increased their individual basal area (BA_t: basal area normalized by the area allocated to eucalypts, i.e., 50% of the plot area; Figure 4a), compared with E100. Interspecific com-

petition suppressed basal area growth in the acacias (Figure 4a) much more than their vertical growth, leading to a higher H/BA_t than in A100 (Figure 4b). From age 3 to 6 years, this ratio was, on average, 54% higher in the MS stand than in A100, and the difference was mainly explained by a smaller average number of stems per acacia tree in MS (2.7 stems/tree) than in A100 (3.7 stems/tree). By contrast, the H/BA_t ratio of the eucalypts was much lower in MS than in E100 (on average, 28% lower in MS than in E100, from age 3 to 6 years; Figure 4b).

Aboveground biomass and net primary production

Since there was no significant difference in BA between treatments over the rotation, differences in wood volume (not shown), wood biomass and total aboveground biomass (Figure 5b and c and Table S3 available as Supplementary Data at *Tree Physiology* Online) were mostly driven by differences in stand height, with lower, intermediate and higher values for A100, MS and E100, respectively. At the end of the rotation, total aboveground biomass was 10.5, 12.2 and 13.9 kg DM m^{-2} in the A100, MS and E100 treatments,
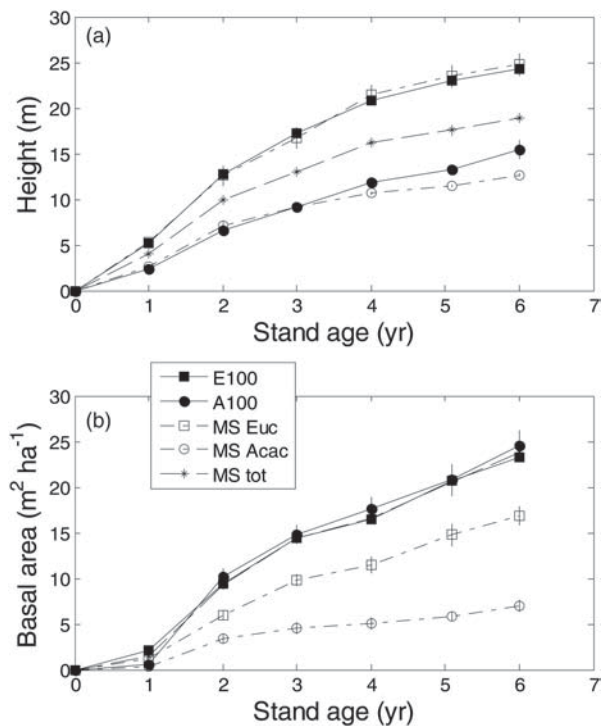
Figure 3. Changes in (a) mean tree height and (b) basal area over the 6 years of the rotation, for the three treatments: E100: monoculture *E. grandis* stands; A100: monoculture *A. mangium* stands; MS: mixed-species *E. grandis/A. mangium* stands. For the MS treatment, mean tree height and basal areas are shown for each species and for the whole stand. Vertical bars represent between-block standard deviations. Note the large differences in tree height and in basal area between eucalypts and acacias in the mixture (resulting in a stratified canopy with a clear domination by eucalypts). Basal areas of E100, A100 and MS were not significantly different (b), despite large differences in tree height (a).
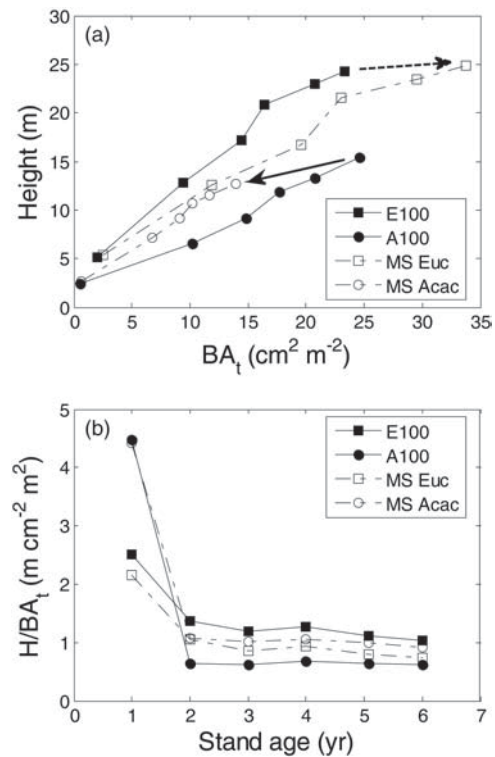

Figure 4. (a) Mean tree height (H) versus mean basal area per tree (BA_t) and (b) the ratio of tree height to basal area of *E. grandis* and *A. mangium* trees in single- or mixed-species plantations. The dashed arrow in (a) shows the changes occurring for *E. grandis* when grown in MS (compared with E100): little change in H but large increases in BA_t are observed. The solid arrow indicates the changes occurring for *A. mangium* when grown in MS (compared with A100): decreases in both H and BA_t are observed. These changes in tree allometry when species are mixed are also shown for different ages in (b).

respectively (see Table S3 available as Supplementary Data at *Tree Physiology* Online). Leaf biomass reached its maximum value 2 years after planting (Figure 5a), and from age 4 years onwards it was significantly higher in the MS plots. This rise in leaf biomass in the MS plots led to a higher leaf/total aboveground biomass ratio in the mixture than in the monocultures for both species: for the last 3 years of the rotation, wood biomass per eucalypt tree in MS was 45% higher, on average, than in E100, while leaf biomass was 74% higher. Over the same period, wood biomass per acacia tree in MS was 53% lower, on average, than in A100, while leaf biomass was only 24% lower.

Litterfall was measured over the whole rotation for the two monocultures, and for the last 2 years in MS. Leaf litterfall (Figure 5d and Table S3) peaked at age 3 years, one year after the leaf biomass peak, and then decreased sharply before

stabilizing at values that were not significantly different between treatments, at ~0.5 kg DM m^{-2} year^{-1} for the last 2 years. The fall of woody products (dead branches and bark) was negligible in the first 2 years, but then increased rapidly in E100, reaching values similar to leaf-fall at 6 years in this treatment (Figure 5e). The very limited woody litterfall in A100, compared with E100, was explained by negligible bark-fall, and by greater retention of dead branches in the acacia canopy (data not shown). Total litterfall (Figure 5f) cumulated over the rotation (6 years) was 4.3 and 3.0 kg DM m^{-2} in E100 and A100, respectively, which was ~31 and 29% of the amount of biomass accumulated aboveground over the same period, in E100 and A100, respectively.

Leaf production (Figure 5g), calculated as annual leaf litterfall, plus the annual change in leaf biomass, peaked at ages 2 and 3, and then decreased with stand age, before stabilizing in
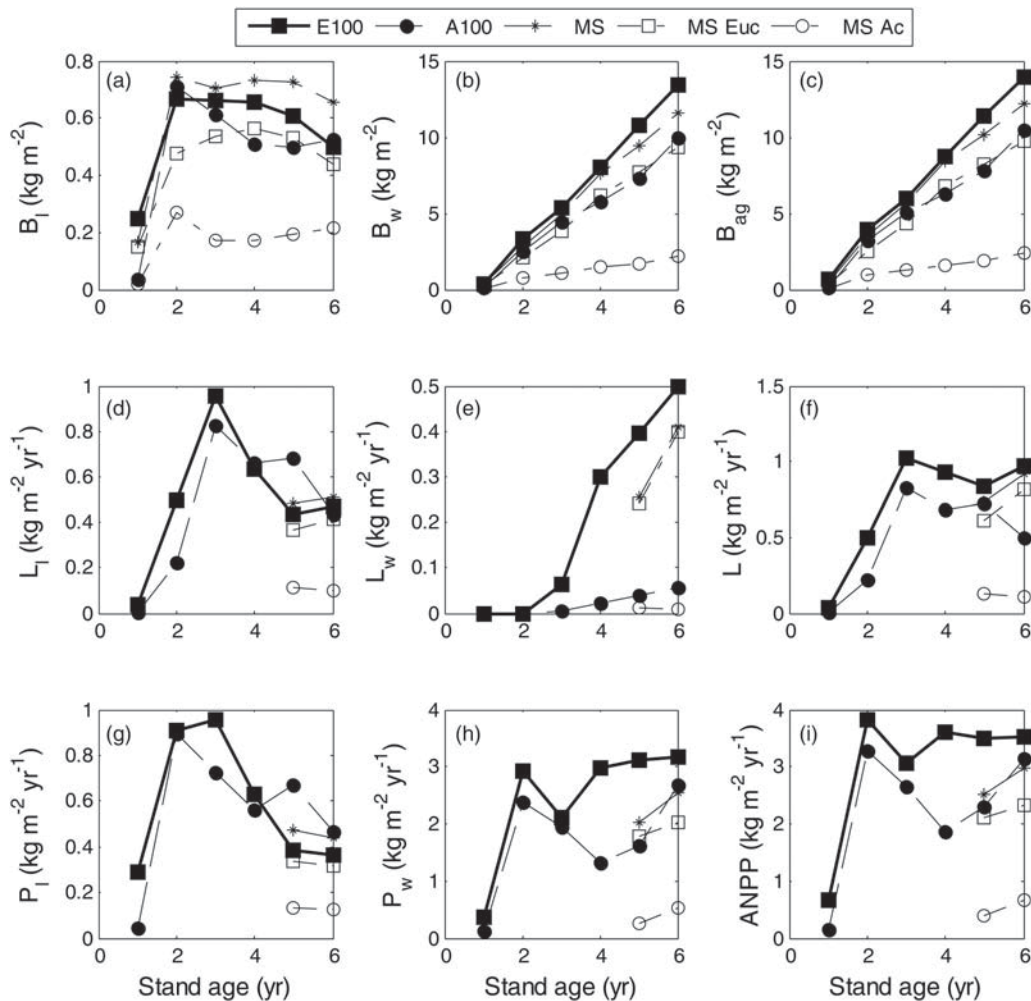
Figure 5. Leaf biomass (B_l, a), leaf litterfall (L_l, d) and leaf production (P_l, g); woody aboveground biomass (B_w, b), woody litterfall (L_w, e) and woody production (P_w, h); aboveground biomass ($B_{ag} = B_l + B_w$, c), litterfall ($L = L_l + L_w$, f) and aboveground net primary production (ANPP = $P_l + P_w$, i) at different stand ages (in years) in single-species *E. grandis* (E100, black-filled squares), *A. mangium* (A100, black-filled circles) plots and mixed-species plots (MS, stars). For the MS treatment the biomass, litterfall and production are given for each species (empty squares for *E. grandis* and empty circles for *A. mangium*). Units for biomass are kg DM m^{-2}. Units for litterfall and production are kg DM m^{-2} year^{-1}. Each point is the mean of three plots per treatment (blocks). Statistics are given in Table S3 available as Supplementary Data at *Tree Physiology* Online.

the last 2 years. Wood production (Figure 5h) and ANPP (Figure 5i) increased sharply from age 1 year to 2 years, after which there was no obvious age-related trend. Cumulated leaf production (over the rotation) in the two monocultures was similar: 3.5 and 3.3 kg DM m^{-2} in E100 and A100, respectively, amounting to 19 and 25% of cumulated ANPP (18.2 and 13.4 kg DM m^{-2}, respectively). The P_l/ANPP ratio decreased with stand age, and was 0.11 and 0.22, on average, in the last 2 years of the rotation (Table 1) for E100 and A100, respectively. Litterfall cumulated over the rotation amounted to 24 and 22% of cumulated ANPP in E100 and A100, respectively, which was close to the ratio observed for the last 2 years of the rotation (26 and 24% for E100 and A100, respectively).

Soil CO$_2$ efflux

Soil CO$_2$ efflux exhibited strong seasonal variations (Figure 6a), with the lowest values (~1 μmol m^{-2} s^{-1}) during the dry/cold season (June–September), and the highest values (~6 μmol m^{-2} s^{-1}) during the wet/warm season (October–May).

Most of this variability was explained by seasonal variations in θ$_v$, and soil temperature (Figure 6b). For most measurement dates, F_s was the lowest in A100, and the highest in MS. Cumulated soil CO$_2$ efflux (Figure 7 and Table 1) was also significantly lower in A100, and higher in MS. From May 2007 to April 2009, the mean annual F_{SCUM} was 0.99, 1.13 and 1.20 kg C m^{-2} year^{-1} for A100, E100 and MS, respectively (Table 1). In MS, F_{SCUM} for position 1 (Figure 2) was 54% higher at collars located close to eucalypt trees than collars located close to acacia trees (data not shown), suggesting higher eucalypt contribution to F_s than acacia.

Total belowground carbon flow

The total belowground C flow was estimated for the last 2 years of the rotation (May 2007–April 2009) using Eq. (2) and measurements of F_{SCUM}, L_{CUM}, and the changes in B_R, C_L and C_T (Table 1). Over these 2 years, L_{CUM} was significantly lower in A100 than in the two other treatments. The difference was mostly due to the lower deposition of woody litter products

Table 1. C fluxes, partitioning and efficiencies (production efficiency and LUE efficiencies) in A100, E100 and MS, over the last 2 years of the rotation. All variables are described in the 'Materials and methods' section. All C fluxes are expressed in kg C m^{-2} year^{-1}; APAR in GJ m^{-2} year^{-1}; LUE in g C MJ^{-1}. TBCF values were computed from F_{SCUM}, L_{CUM}, ΔB_R, ΔC_L and ΔC_T using Eq. (2). GPP was computed from TBCF and ANPP using Eq. (4). Plot means are given with standard deviations (SE). Values followed by different letters are significantly different at $P = 0.05$.

| Variable	A100	E100	MS		
			Acacias	Eucalypts	Stand
P_l	0.283 ± 0.016 a	0.187 ± 0.005 c	0.065 ± 0.012	0.163 ± 0.010	0.228 ± 0.020 b
P_w	0.999 ± 0.176 b	1.437 ± 0.073 a	0.181 ± 0.009	0.864 ± 0.107	1.045 ± 0.116 b
ANPP	1.282 ± 0.192 b	1.624 ± 0.073 a	0.246 ± 0.019	1.027 ± 0.117	1.273 ± 0.133 b
ΔB_w	0.976 ± 0.178 b	1.236 ± 0.082 a	0.176 ± 0.007	0.719 ± 0.085	0.895 ± 0.092 b
P_l/ANPP	0.223 ± 0.020 a	0.115 ± 0.006 c	0.262 ± 0.032	0.160 ± 0.009	0.180 ± 0.009 b
P_w/ANPP	0.777 ± 0.020 c	0.885 ± 0.006 a	0.738 ± 0.032	0.840 ± 0.009	0.820 ± 0.009 b
ΔB_w/ANPP	0.759 ± 0.024 a	0.761 ± 0.020 a	0.716 ± 0.036	0.700 ± 0.004	0.703 ± 0.008 b
F_{SCUM}	0.994 ± 0.054 a	1.133 ± 0.090 b			1.199 ± 0.085 b
L	0.302 ± 0.006 b	0.420 ± 0.023 a	0.058 ± 0.014	0.340 ± 0.031	0.398 ± 0.041 a
ΔB_r	0.164 ± 0.027 c	0.243 ± 0.017 a	0.017 ± 0.001	0.194 ± 0.016	0.211 ± 0.017 b
ΔC_L	−0.031 ± 0.061 b	0.181 ± 0.035 a			0.147 ± 0.015 a
ΔC_T	−0.044 ± 0.005 a	−0.031 ± 0.012 a			−0.027 ± 0.017 a
TBCF	0.781 ± 0.097 b	1.097 ± 0.133 a			1.132 ± 0.066 a
TACF	2.419 ± 0.363 b	3.065 ± 0.139 a	0.464 ± 0.036	1.938 ± 0.220	2.402 ± 0.252 b
GPP	3.200 ± 0.430 b	4.162 ± 0.260 a			3.534 ± 0.286 ab
ΔB_w/TBCF	1.250 ± 0.178 a	1.127 ± 0.098 a			0.791 ± 0.071 b
ANPP/TBCF	1.642 ± 0.197 a	1.480 ± 0.120 a			1.125 ± 0.111 b
P_l/GPP	0.089 ± 0.006 a	0.045 ± 0.003 c			0.065 ± 0.004 b
P_w/GPP	0.311 ± 0.016 b	0.345 ± 0.008 a			0.295 ± 0.010 b
ΔB_w/GPP	0.304 ± 0.017 a	0.297 ± 0.010 a			0.253 ± 0.006 b
TBCF/GPP	0.245 ± 0.023 b	0.263 ± 0.016 b			0.321 ± 0.022 a
LAI	3.479 ± 0.283 b	3.681 ± 0.117 b	1.525 ± 0.120	3.145 ± 0.430	4.671 ± 0.325 a
APAR	1.996 ± 0.107 b	2.112 ± 0.026 b	0.813 ± 0.049	2.059 ± 0.221	2.872 ± 0.182 a
GPP/LAI	0.919 ± 0.074 b	1.131 ± 0.076 a			0.756 ± 0.013 b
LUE$_{\Delta B_w}$	0.489 ± 0.065 b	0.585 ± 0.045 a	0.216 ± 0.021	0.349 ± 0.011	0.312 ± 0.013 c
LUE$_{ANPP}$	0.642 ± 0.066 b	0.769 ± 0.044 a	0.304 ± 0.032	0.499 ± 0.017	0.443 ± 0.021 c
LUE$_{GPP}$	1.601 ± 0.153 b	1.972 ± 0.147 a			1.230 ± 0.022 c
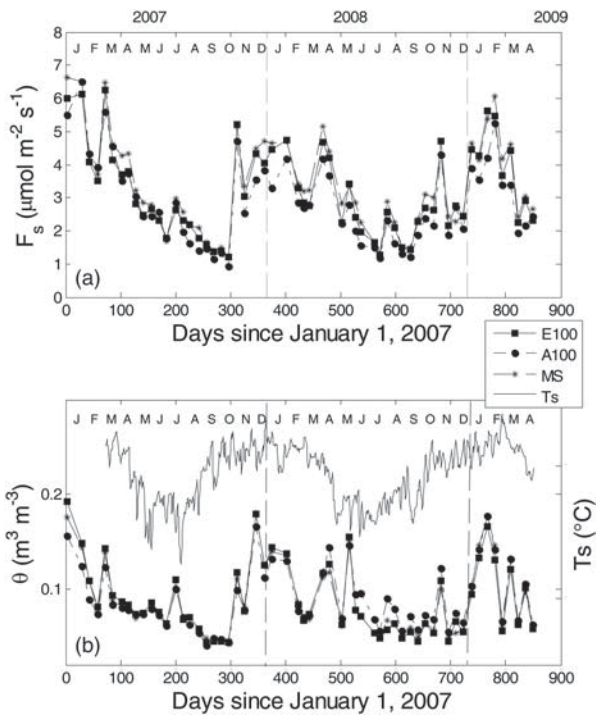
Figure 6. Soil CO_2 efflux (F_S, a) and soil water content (θ_v, b) measured every 2 weeks over the last 2 years of the rotation (from January 2007 to April 2009), in single-species *E. grandis* (E100, black-filled squares), *A. mangium* (A100, black-filled circles) plots and mixed-species plots (MS, stars). Each point is the mean of 27 measurements for E100 and A100 (nine collars per plot and three plots per treatment), and 54 measurements for MS (18 collars per plot and three plots; one per block). The mean daily soil temperature measured in MS at a depth of 4 cm (T_s) is also presented (b). Mean daily values were obtained from 48 semi-hourly values ×4 thermocouples.
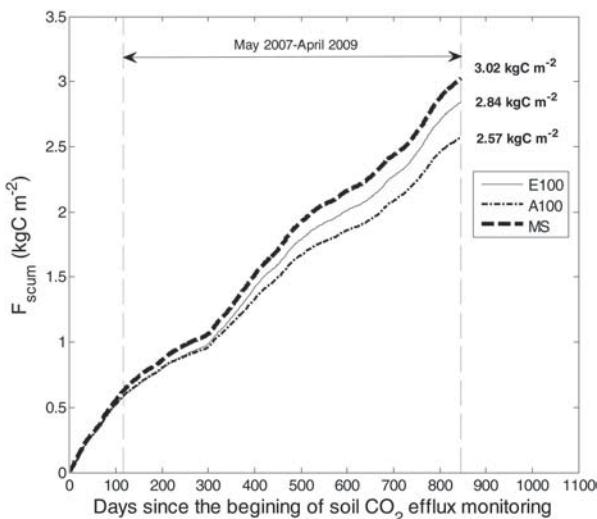

Figure 7. Cumulative soil CO_2 efflux from January 2007 to April 2009 in single-species *E. grandis* (E100) and *A. mangium* (A100) plots, and mixed-species (MS) plots. Data collected over the last 2 years of the rotation (from May 2007 to April 2009; horizontal double arrow) were used to compute total belowground C flux (Eq. (2)).

(branches and bark). Forest floor C, C_L, decreased slightly from 4 to 6 years after planting in A100 (−0.03 kg C m^{-2} year^{-1}), but increased in the other two treatments (Table 1). This increase was mainly due to the accumulation of coarse litter fragments (dead branches from eucalypt trees; data not shown). The C efflux resulting from the decomposition of coarse roots and stumps from the previous rotation ($\Delta C_T/\Delta t$) was not significantly different in the three treatments (Table 1), and amounted, on average, to only 3.1% of F_{SCUM}. The coarse and medium root biomass increment (ΔB_R) was, after F_{SCUM} and L_{CUM}, the third largest term in Eq. (2), and was lowest in A100, and highest in E100. TBCF was significantly lower in A100 (0.78 kg C m^{-2} year^{-1}) than in E100 (1.10 kg C m^{-2} year^{-1}) and MS (1.13 kg C m^{-2} year^{-1}).

ANPP/TBCF, ΔB_w/ANPP, ΔB_w/TBCF ratios

The ANPP/TBCF ratio in MS was 24 and 33% lower than in E100 and A100, respectively (Table 1): for each kg of C allocated belowground, MS plots produced 1.12 kg C of plant tissues aboveground (wood, bark and leaves), much less than in A100 and E100 (1.48 and 1.64 kg C, respectively). The fraction of ANPP allocated to the woody biomass increment (ΔB_w) was also significantly lower in MS than in the two monoculture treatments. This lower ΔB_w/ANPP ratio (and higher L_{CUM}/ANPP) in MS compared with E100 and A100 was observed at stand level, and for the two species. Due to lower ANPP/TBCF and ΔB_w/ANPP ratios, the ΔB_w/TBCF ratio was also much lower in MS than in the two monoculture treatments. For each kg of C allocated belowground, MS plots accumulated only 0.79 kg C of wood aboveground, which was 30 and 37% less than in E100 and A100 (1.13 and 1.25 kg C, respectively; Table 1).

GPP partitioning

GPP was 30% higher in the monoculture *Eucalyptus* plots (4.16 kg C m^{-2} year^{-1}) than in the monoculture *Acacia* plots (3.20 kg C m^{-2} year^{-1}; Table 1). GPP in MS (3.53 kg C m^{-2} year^{-1}) was intermediate (15% lower than in E100, and 10% higher than in A100). The fraction of GPP allocated belowground (TBCF/GPP ratio) in the two monocultures was not significantly different and amounted to ~0.25 (Table 1). This ratio was higher in the MS plots (0.32). In the two monoculture treatments, the fraction allocated to wood production (P_w/GPP) was higher than the fraction allocated belowground (TBCF/GPP). In contrast, MS plots allocated a higher fraction of GPP belowground than to wood production. The fraction of GPP allocated to leaf production was highest in A100 (0.089), lowest in E100 (0.045) and intermediate in MS (0.065; Table 1).

The 21% lower growth (ΔB_w) in A100 compared with E100 was almost entirely explained by the 23% lower GPP. In contrast, the 28% lower ΔB_w in MS than in E100 was explained both by a 15% lower GPP and by a 15% lower fraction of GPP allocated to wood biomass accumulation (Table 1).

LAI, APAR and LUE

LAI and APAR in the MS stands were much higher (30 and 40% higher, respectively) than in the two monocultures (Table 1). This strong increase in APAR compared with monocultures did not lead to increased production, thus resulting in light-use efficiencies for GPP, ANPP and wood increment that were much lower in the MS stands than in A100 and E100. Light-use efficiencies in E100 were higher than in A100. In MS, the decrease in LUE for wood increment (ΔB_w/APAR) compared with monocultures was observed for both species, but was more marked for the dominated acacia species (−56%) than for eucalypts (−41%).

Discussion

Production and C partitioning in monocultures of *E. grandis* and *A. mangium*

The aboveground woody biomass (B_w) at the end of the 6-year rotation in E100 (13.4 kg DM m^{-2}) was similar to that reported by Epron et al. (2012) for a nearby 6-year-old *E. grandis* stand (15.2 kg DM m^{-2}). The mean annual B_w increment (ΔB_w) over the full rotation in A100 (1.66 versus 2.24 kg DM m^{-2} year^{-1} in E100) was only slightly higher than the ΔB_w reported for *A. mangium* stands in Congo (1.55 kg DM m^{-2} year^{-1}; Bernhard-Reversat et al. 1993) in an area where the mean annual ΔB_w of adjacent eucalypt plantations ranges from 1.1 to 1.5 kg DM m^{-2} year^{-1} (Laclau et al. 2010a, 2010b).

Despite large differences in wood production and ANPP between eucalypt and acacia monocultures, we found little difference in F_{SCUM} (Table 1), as found by Forrester et al. (2006b). We also found little difference between the two species for leaf biomass and for leaf production cumulated over the rotation. Laclau et al. (2008) reported a strong linear relationship between fine root biomass and leaf biomass, which was common for the two species. These results suggest that not only leaf, but also fine root biomass were similar in E100 and A100. This was confirmed by intensive sampling at age 5 years in the same plots: fine root biomass (diameter <3 mm) down to a depth of 2 m was 0.35 kg DM m^{-2} in both A100 and E100. In contrast, the biomasses of coarse roots (diameter > 10 mm) and medium-sized roots (3 mm < diameter ≤ 10 mm) were higher in E100 than in A100 (2.18 versus 0.95 kg DM m^{-2} and 0.22 versus 0.13 kg DM m^{-2}, respectively; Laclau *et al.* 2012).

TBCF was similar in E100 (1.1 kg C m^{-2} year^{-1}) and in a nearby *E. grandis* stand (0.95 kg C m^{-2} year^{-1}; Epron et al. 2012), and fell within the range of values reported for other *Eucalyptus* plantations in Brazil (0.42–1.00 kg C m^{-2} year^{-1}; Ryan et al. 2010; 0.50–1.23 kg C m^{-2} year^{-1}; Campoe et al. 2012). In contrast to previous studies that reported higher TBCF in N$_2$-fixing tree plantations than in adjacent eucalypt

plantations (1.54 kg C m^{-2} year^{-1} in *Albizia falcataria* (L.) Fosberg stands versus 1.18 kg C m^{-2} year^{-1} in adjacent *E. saligna* stands in Hawaii; Binkley and Ryan 1998; 1.58 kg C m^{-2} year^{-1} in *Acacia mearnsii* stands versus 1.46 kg C m^{-2} year^{-1} in adjacent *E. globulus* stands in Australia; Forrester et al. 2006b), the TBCF values estimated in our *A. mangium* monoculture (0.78 kg C m^{-2} year^{-1}) were 29% lower than in E100. About 25% of the difference in TBCF between the two species was explained by higher medium and coarse root biomass increment in E100 than in A100, but it was not known as to how much of the remaining difference was explained by differences in fine root production, exudation or root respiration. In the A100 treatment, a fraction of the TBCF was allocated to N$_2$ fixation: most of the reported values for the C cost of this process range between 4 and 6 kg C (kg N$_2$ fixed)$^{-1}$ (Cannell and Thornley 2000). Estimated N$_2$ fixation in A100 at age 2 years was 26 kg N ha^{-1} year^{-1} (Bouillet et al. 2008) amounting to a C cost of ~0.013 kg C m^{-2} year^{-1} (~2% of TBCF). Specific root respiration is known to decrease when root diameter increases (Marsden et al. 2008a, 2008b, Chen et al. 2009), and to rise with N concentrations in the roots (Tjoelker et al. 2005, Chen et al. 2010), but generally with lower respiration rates per unit N in legumes than other species (Tjoelker et al. 2005). For a given root diameter, Chen et al. (2009) found higher specific respiration rates in *Acacia crassicarpa* (A. Cunn. ex Benth.) roots than in *Eucalyptus urophylla* (S. T. Blake) roots due to higher N concentrations, but the difference in specific respiration rates was offset by >3 times higher coarse root biomass in *E. urophylla* stands, resulting in higher stand-level root respiration rates in eucalypt stands than in acacia stands. In our study, the 2.2 times higher coarse plus medium root biomass in E100 than A100 may have led to higher root respiration, which may account for the higher TBCF in E100 than in A100.

We put forward the hypothesis that the difference in wood production between the two species was partly explained by differences in C allocations. Such species-related differences in C allocation were reported by Binkley and Ryan (1998) for 16-year-old plantations of *E. saligna* and N$_2$-fixing *A. falcataria*: despite the same NPP for the two species (2.0 kg C m^{-2} year^{-1}), stem production was higher in *Eucalyptus* stands than in *Albizia* plantations due to a larger fraction of NPP allocated to stem production (45% of NPP versus 34% for *Albizia* trees) and a smaller fraction of NPP allocated to belowground production (29% of NPP versus 41% for *Albizia*). Their estimates of belowground NPP (BNPP) were based on TBCF measurements and an assumed CUE for belowground production of 0.5 for both species, which is the same CUE value than that found by Litton and Giardina (2008) for tropical forest ecosystems. With the same assumption, we estimated BNPP at 0.55 and 0.39 kg C m^{-2} year^{-1}, and NPP (ANPP + BNPP) at 2.17 and 1.67 kg C m^{-2} year^{-1} for E100 and A100, respectively. The resulting ΔB_w/NPP (0.57 for E100 and 0.58 for A100) and BNPP/NPP

ratios (0.25 and 0.23 for E100 and A100, respectively) were similar for the two species. Consequently, unlike the results obtained by Binkley and Ryan (1998), the species differences in wood production in our study were not explained by differences in C allocation, but by differences in NPP and GPP, which were 30% higher in *Eucalyptus* stands than in *Acacia* stands. Binkley and Ryan (1998) suggested that lower soil P supply under *Albizia*, which requires more P than eucalypts, may be partially responsible for the high BNPP/NPP ratio. Abundant initial P fertilization in all the treatments probably prevented P limitations in our experiment.

Our estimate of GPP for E100 (4.16 kg C m^{-2} year^{-1}) was similar to the value reported by Epron et al. (2012) for a nearby fertilized stand (4.44 kg C m^{-2} year^{-1}), and in the upper range of values reported by Ryan et al. (2010) for different Brazilian eucalypt plantations (2.89–4.24 kg C m^{-2} year^{-1}). These estimates of GPP for E100, and for A100 (3.20 kg C m^{-2} year^{-1}), were obtained using Eq. (4), assuming a constant CUE of 0.53. This value was reported for *E. saligna* plots in Hawaii (Giardina et al. 2003). Differences in the CUE of different forests have been reported (DeLucia et al. 2007, Litton et al. 2007), but most of the differences were related to stand age (DeLucia et al. 2007) and climate (DeLucia et al. 2007, Litton et al. 2007). We are not aware of any studies that compared the CUE of fast-growing eucalypts and N$_2$-fixing trees. CUE values reported for legume crops do not seem to differ from those of other crops (Amthor 2000, Albrizio and Steduto 2003). The only value reported by DeLucia et al. (2007) for a N$_2$-fixing tree (*Alnus rubra*) was 0.52. Differences in CUE between *Eucalyptus* and *Acacia* are likely, but not to the point of offsetting the estimated differences in GPP or NPP between A100 and E100 (for NPP, the differences cannot be offset, whatever the value of CUE for belowground production).

The 19% lower production efficiency (GPP/LAI ratio) in A100 than in E100, which resulted from the lower GPP despite similar LAI, was consistent with lower photosynthetic capacities (lower maximum carboxylation rates and maximum rates of electron transport) for *A. mangium* leaves than *E. grandis* leaves, shown by leaf gas exchange measurements in A100 and E100 (unpublished results).

For both species, ~25% of GPP was allocated belowground, which is in the lower range of the values reported by Litton et al. (2007), and Litton et al. (2008), but similar to the values reported by Epron et al. (2012) (21% at a nearby *Eucalyptus* stand), or by Ryan et al. (2010) (11–30%) and Campoe et al. (2012) (14–31%) for other eucalypt stands in Brazil. This ratio (TBCF/GPP) was reported to decrease with nutrient availability (Keith et al. 1997, Giardina et al. 2003, Epron et al. 2012), and forest productivity (Litton et al. 2007). A low ratio is therefore not surprising for our fast-growing *Acacia* and *Eucalyptus* plantations. By contrast, partitioning to wood production was reported to increase with conditions favouring high GPP

(Litton et al. 2007). The values obtained in A100 (0.31) and E100 (0.34) are higher than the values (0.08–0.31) reported by Litton et al. (2007), but are similar to the values reported for other fast-growing eucalypt plantations in Brazil (0.26–0.46; Ryan et al. 2010, Epron et al. 2012).

Partitioning to foliage production was reported to decrease (from 0.10 to 0.05) with K fertilization at nearby *Eucalyptus* stands (Epron et al. 2012), but showed little variation across different fertilized stands in Brazil (0.05 to 0.07; Ryan et al. 2010). The values obtained for E100 (0.05) and A100 (0.09) fall within the range of values reported by Litton et al. (2007) for other forests (0.04–0.13).

Effect of mixing species on stand structure, C uptake and C partitioning

Mixing *A. mangium* and *E. grandis* trees in the same stands, without altering total stand density, led to ontogenic shifts and structural changes that affected both species. One of the most evident morphological changes at tree level was the increase in the H/BA_t ratio for the acacias (as previously observed in other MS *Acacia–Eucalyptus* forests; Hunt et al. 2006), which was associated with a reduced number of stems per tree (compared with A100), and the decrease in the H/BA_t ratio for eucalypts (compared with E100). Eucalypt trees rapidly dominated the acacias, leading to a stratified canopy, as also reported in previous studies (Hunt et al. 2006). The establishment of such a stratified canopy, with the pendulous eucalypt leaves in the upper layer and the more horizontal acacia leaves in the lower layer (le Maire et al. 2012), was shown to increase light interception in MS *Eucalyptus–Acacia* forests (Hunt et al. 2006, Forrester et al. 2006a, le Maire et al. 2012).

Unlike some previous studies (e.g., Binkley et al. 2003), the decrease in the growth of dominated N$_2$-fixing trees in the MS stands was not offset by the higher growth of *Eucalyptus* trees, thus leading to 14% lower mean wood production in the MS stands, compared with E100. The productivity of mixtures of N$_2$-fixing and non-fixing tree species remains unaffected or even decreases at N-rich sites compared with non-fixing monoculture plantations (Binkley 1992). Even though a significant tree response to N fertilization was observed in the first 2 years after planting, wood biomass at the end of the rotation showed that N limitation was low at our site (Laclau et al. 2008, 2010a, le Maire et al. 2012). The lack of transgressive aboveground over-yielding (Fridley 2001) might result from the fact that N was not the resource that most limited tree growth at our site.

Mixing the two species led to strong increases in leaf biomass, LAI and APAR in MS compared with acacia and eucalypt monocultures, and these increases were mirrored belowground by strong rises (+25%) in fine root biomass (0.44 kg DM m^{-2} in MS versus 0.35 kg DM m^{-2} in A100 and E100; Laclau et al. 2012). Increases in LAI in mixtures were previously reported

by Binkley (1992) for plantations of Douglas fir with Sitka alder that had a higher LAI than pure stands of Douglas fir, or by Forrester et al. (2010) in mixtures of *E. globulus* and *A. mearnsii* in Australia. The leaf area per tree (and the fine root biomass per tree; Laclau et al. 2012) of eucalypts in our MS stands was almost twice as high as in E100. As a result, eucalypt LAI was only 15% lower in MS than in E100, despite a tree spacing that was twice as high (18 versus 9 m^2 per eucalypt tree in MS and E100, respectively), thus resulting in a higher total (*Eucalyptus + Acacia*) LAI in MS than in acacia and eucalypt monocultures. Thinning experiments in *Eucalyptus nitens* (H. Deane & Maiden) plantations in Australia (Medhurst and Beadle 2001) showed that, 7 years after thinning, the LAI of plantations with a residual stocking of 400 trees ha^{-1} was 24% lower than in stands with a density of 800 tree ha^{-1}. Their best-fit equation between stocking and LAI predicts a 12% reduction in LAI associated with a decrease in stocking from 1100 trees ha^{-1} (as in E100) to 550 tree ha^{-1} (stocking of eucalypts in MS), similar to the 15% decrease observed in our study. Consequently, in MS, the leaf area of the eucalypts was probably similar to the LAI expected for monoculture plantations with the same stocking, thus suggesting that acacias had no effect on eucalypt leaf area.

The shift in canopy structure (le Maire et al. 2012) and the higher LAI in MS compared with the monocultures resulted in a higher APAR, but it is unlikely that the higher fine root biomass in MS led to greater water uptake than in E100. Monitoring of actual evapotranspiration (AET) by eddy-covariance and of soil water content (SWC) to a depth of 10 m at a nearby *E. grandis* plantation of the same age and planted on similar soils as E100 showed that AET (and GPP) was strongly limited by soil water availability for the last 2 years of the rotation, and all the annual rainfall was evapotranspired (Nouvellon et al. 2011). Measurements of SWC down to a depth of 3 m in E100 confirmed the dry soil conditions at the end of the rotation (Laclau et al. 2012). The lower GPP in MS (3.53 kg C m^{-2} year^{-1}) than in E100 (4.16 kg C m^{-2} year^{-1}), despite higher LAI and APAR values, was probably the result of greater water stress and stomatal closure in MS than in E100, due to lower soil water availability per unit of leaf area. Increased water stress and stomatal closure in MS would also explain their low LUE$_{gpp}$ (1.23 g C MJ^{-1} APAR in MS versus 1.97 g C MJ^{-1} APAR in E100). Lower water availability in rainfed plantations compared with irrigated eucalypt plantations in Brazil was found to decrease LUE$_{gpp}$ from 1.80 to 1.59 g C MJ^{-1} APAR (Ryan et al. 2010).

As for leaf biomass and LAI, diversity has been reported to lead to fine root over-yielding in comparison with single-species forests (Schmid 2002, Brassard et al. 2011, Laclau et al. 2012). The higher fine root biomass in MS than in the monocultures may explain why the TBCF was as high in MS as in E100, despite lower total root biomass (Laclau et al. 2012) and ΔB_R

(Table 1). Fine roots have higher specific respiration rates than coarse roots (Marsden et al. 2008a), and thus contribute to a large proportion of stand root respiration (Marsden et al. 2008b) despite their low contribution to total root biomass. The fast turnover of fine roots in tropical plantations (e.g., Jourdan et al. 2008) may also account for a large fraction of TBCF. Although not measured in our experiment, fine root production may be estimated as the difference between BNPP and ΔB_R. Assuming a CUE of 0.5 for belowground production (Binkley and Ryan 1998, Litton and Giardina 2008), BNPP in MS was 0.57 kg C m^{-2} year^{-1} (versus 0.55 and 0.39 kg C m^{-2} year^{-1} in E100 and A100, respectively), leading to higher fine root production estimates in MS (0.36 kg C m^{-2} year^{-1}, 31% of TBCF) than in E100 (0.31 kg C m^{-2} year^{-1}; 28% of TBCF) and in A100 (0.23 kg C m^{-2} year^{-1}; 29% of TBCF). The lower ΔB_R/BNPP ratio in MS (0.37) than in E100 (0.44) and in A100 (0.42) was reflected aboveground by a lower ΔB_w/ANPP ratio in MS (0.70) than in E100 (0.76) and A100 (0.76). A larger proportion of NPP was allocated to above- and belowground litter production, and a smaller proportion to growth (C accumulation in wood biomass) in the mixture than in the monoculture plantations (ΔB_w/NPP ratio of 0.49 in MS versus 0.57 and 0.58 in E100 and A100, respectively, and ($\Delta B_w + \Delta B_R$)/NPP ratio of 0.60 in MS versus 0.68 in E100 and A100). This shift in the proportion of NPP allocated to growth versus short-lived organs (leaves and fine roots) was also associated with a shift in the proportion of NPP allocated belowground as opposed to aboveground: the BNPP/NPP ratio was higher in MS (0.31) than in the two monocultures (0.25 in E100 and 0.23 in A100). Thus, as hypothesized, the lower wood increment in the mixture compared with E100 was partly explained by shifts in C partitioning. Interestingly, the shifts in production and C partitioning observed in our plantations were opposite to those observed by Forrester et al. (2006b) in southern Australia. They found that the higher wood production in mixtures of eucalypts and acacias compared with monocultures was associated with a higher ANPP/TBCF in the mixtures. In our study, the lower wood production in MS than in E100 was associated with a lower ANPP/TBCF ratio. Litton et al. (2007) found that partitioning decreases to wood and increases to belowground with a decreasing GPP, across a large range of forest ecosystems. Consistently with this trend, the lower wood production in MS than in E100 resulted from a lower GPP, associated with lower partitioning to wood increments (0.25 in MS versus 0.30 in E100), and greater partitioning belowground (0.32 in MS versus 0.26 in E100). Our results showed that the lower LUE for stem production in the mixture than in E100 (le Maire et al. 2012) resulted from a 38% lower LUE$_{gpp}$, and from a 15% lower ΔB_w/GPP ratio. Both species had lower LUE values for wood increments (ΔB_w/APAR) in MS than in their respective monoculture, with a more pronounced decrease for the dominated acacia trees than for the dominant eucalypt trees.

Our methodology did not enable us to assess for each species how much of the decrease in $LUE_{\Delta B_w}$ was attributable to a decrease in LUE_{gpp} and to shifts in C allocation, since TBCF and GPP were not estimated separately for each species in the mixture. However, it is likely that water limitations affected the LUE_{gpp} of both species, and that C allocation shifts also occurred for both species, as suggested by the lower ΔB_w/ANPP in MS than in the monocultures observed for both species.

Conclusion

Our results showed that in monocultures, *A. mangium* and *E. grandis* exhibited similar C allocation patterns, and the differences in wood production were mainly explained by differences in NPP and GPP. Mixing the two species resulted in strong rises in leaf biomass and in APAR, but the higher APAR did not lead to a higher GPP (compared with E100), likely as a result of strong water limitations. The lower wood production in the mixture than in *E. grandis* monoculture plantations was accounted for by lower GPP and NPP values, as well as shifts in C allocations from above- to belowground, and from growth to litter production. The low response of *E. grandis* to N fertilization at our site (which may result from water limitations) might have dampened the potential benefits of introducing N_2-fixing tree species in eucalypt plantations. Further studies should therefore assess the potential of mixed-species plantations in other tropical areas where *Eucalyptus* growth is more limited by N availability, and water limitations are less severe than in our area. Further studies should also (i) compare the CUE of the two species, based on measurements of NPP and respiration, since our calculations of GPP were based on the hypothesis of a constant CUE, while some differences are likely between the two species; (ii) develop methodologies to assess the GPP and TBCF of each species in the mixtures in order to gain a better understanding of the effects of interspecific interactions on the production and C allocation of the two species in the mixed-species stands; (iii) investigate interspecific competition for water in the mixtures, and their effects on C allocations.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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