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Tree and stand light use efficiencies over a full rotation of single- and mixed-species *Eucalyptus grandis* and *Acacia mangium* plantations

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ABSTRACT

Understanding the light absorption and light use efficiency of each species at the tree scale is essential to disentangle the effects of intra- and inter-species interactions on productivity in mixed-species forest plantations. A complete randomized block design was set up using *Eucalyptus grandis* (E) and *Acacia mangium* (A), which is a N₂-fixing species, planted in monospecific stands (100A, 100E) and in additive (25A:100E, 50A:100E, 100A:100E) and replacement (50A:50E) mixtures. Tree size and biomass were monitored over the complete rotation (6 years). The absorbed photosynthetically active radiation (APAR) for each tree in the experiment was simulated over the full rotation with the MAESTRA model. Measurements of tree leaf area, leaf angle distributions, leaf area density, and leaf and soil optical properties were performed to parameterize this model. The APAR and the ratio of stem biomass increment divided by the APAR (which is a measure of the Light Use Efficiency [LUE] for stem production) were calculated at tree and plot scales for each year of the rotation. The LUE of the 100E stand increased with age until stabilizing at 4 years of age, while the LUE of the 100A stand decreased between 2 and 4 years of age and increased between the two last years of the rotation. *Eucalyptus* trees dominated *Acacia* trees in mixed plantations. The stratification of the canopy led to an increase of stand Leaf Area Index (LAI) and APAR compared to monospecific plantations. However, both *Eucalyptus* and *Acacia* LUE decreased at the end of the rotation in the mixed-species stands, with the decrease occurring more markedly in *Acacia*, and the final stem biomass of the stand was not enhanced in mixed-species plantations compared with the average of the pure stands. Our results indicate that a stratified canopy may offer the potential benefit of capturing more light in mixed-species forests, but this may be negated if another resource deficiency prevents trees from converting intercepted radiation into dry matter. Mixed-species plantations should be established at sufficiently rainfed sites to maximize LUE, and appropriate fertilizer regimes should be applied.

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1. Introduction

Most forest plantations are currently grown as monocultures. In tropical countries, highly productive *Acacia mangium* (Willd.) and *Eucalyptus grandis* Hill ex Maid. monospecific plantations are managed over several million hectares (FAO, 2006; Yamashita et al., 2008). Mixed-species plantations can be used to increase the overall stand productivity through complementarity and/or facilitation processes (Forrester et al., 2006; Kelty, 2006). Species with complementary rooting traits, contrasting vertical growth rates, different crown structures or foliar phenology may increase resource capture by taking advantage of complementary niches (Kelty, 2006; Cardinale et al., 2007). Resource use efficiency is estimated as the

quantity of gross or net production per unit of resource used (e.g., water use efficiency, light use efficiency, nutrient use efficiency). While resource use efficiency may increase with resource use (Binkley et al., 2004), mixed-species plantations may also use the resource more efficiently through facilitation mechanisms (Kelty, 2006). For example, planting N₂-fixing tree species with non-N₂-fixing tree species may enhance N soil availability and increase the growth of the non-N₂-fixing trees (Kaye et al., 2000; Richards et al., 2010). Many studies have shown that N-fixing species may have a positive effect on the overall productivity of mixed forest plantations (e.g., Binkley et al., 1992; Khanna, 1997; Bauhus et al., 2000, 2004; Forrester et al., 2006). However, inter-specific interactions depend on species associations (Forrester et al., 2006), soil fertility (Boyden et al., 2005), site climatic characteristics, abiotic stress factors (Forrester et al., 2011; Moore et al., 2011), and stand ages (Forrester et al., 2011). While many of these

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studies have shown a positive effect of tree diversity on forest productivity, especially with N-fixing species, the advantages gained through complementarity or facilitation processes are sometimes counterbalanced by competition for light, water, or nutrient resources (Khanna, 1998; Forrester et al., 2005; Cardinale et al., 2007). Furthermore, mixing species can change how plants allocate resources to their constitutive components (Forrester et al., 2006; Richards et al., 2010).

To improve our understanding of the processes influencing tree growth in mixed forest plantations, it is necessary to disentangle the competition for light, water, nutrients, and the effects of intra- and inter-specific competition on carbon partitioning between tree components. In this study, we focus on the effect of competition for light on mixed-species plantations of *A. mangium* (N-fixing trees) and *E. grandis* trees in Sao Paulo State, Brazil (Bouillet et al., 2008; Laclau et al., 2008).

The objective of our study was to gain insight into the light absorption behavior of these fast-growing tree species in mixed-species plantations. We aimed to answer three specific questions regarding light use in mixed-species forests:

- Is the growth reduction of the shortest species in a stratified canopy caused by a reduction in the amount of absorbed radiation?
- What is the influence of inter-specific interactions on the conversion of absorbed radiation to stem biomass for each species (i.e., their light use efficiency)?
- What are the dynamics of light use efficiency during tree development for each species?

We conducted a joined modeling and experimental approach based on the intensive monitoring of an additive and a replacement series of *A. mangium* and *E. grandis* over a full rotation. A three-dimensional (3D) model, MAESTRA, was used to estimate the absorbed radiation of each individual tree in the trial over the 6-year rotation period, and the results were then compared to the measurements of the stem growth and leaf area of each individual tree. The effects of inter-tree competition for light on stem growth were analyzed by separating the influence of the following: (1) tree leaf area, (2) absorbed radiation per unit of leaf area, and (3) stem growth per unit of absorbed radiation (i.e., variations in light use efficiency).

2. Materials and methods

2.1. Study site

2.1.1. Ecological situation

This study was carried out in southern Brazil (23°02'S, 48°38'W) at the Itatinga experimental station. The long-term annual rainfall of the study area is 1360 mm, there is a cold season from June to September, and the average annual temperature is 19 °C, with minimum temperatures dropping below 5 °C for a few days every year. The average annual PAR from 2003 to 2009 was 2760 MJ m⁻² year⁻¹. The site has a gentle, undulating topography that is typical of the São Paulo Western Plateau. The experiment was located on a plateau (slope <3%). The soils were Ferralsols (FAO classification) developed on cretaceous sandstone. The textural uniformity of the soil was high (clay content around 13% in the A1 horizon and ranging from 20% to 25% in the 1–6 m profile). The effective cation exchange capacity ranged from 2 to 20 mmol_c kg⁻¹ in the upper 3 m of soil, and the amounts of exchangeable “bases” were <2 mmol_c kg⁻¹ beyond a depth of 5 cm (Voigtlaender et al., 2012). The experiment was conducted in a coppiced *E. saligna* (Sm.) plot that was not fertilized from 1940 to 1997. The stumps were

devitalized, and *E. grandis* seedlings were planted in the plot in 1998 and received low fertilizer inputs (30, 26 and 25 kg ha⁻¹ of N, P and K, respectively).

2.1.2. Experimental layout

The *E. grandis* stand was harvested in December 2002. Only the boles were removed from the plot, and slash were spread uniformly in the field. A complete randomized block design was set up in May 2003 with 7 treatments and 4 blocks to assess the influence of an *A. mangium* understorey on the growth of *E. grandis* seedlings (a highly productive half-sib family selected by the Suzano Company). An additive and a replacement series were set up in the same experiment to address different objectives. The additive series was used to assess the response of *Eucalyptus* trees to contrasted densities of *Acacia* trees growing as an understorey, and the replacement series (between two species used for cellulose production) was used to analyze the consequences of intra- and inter-specific competition on the development of each species. Each plot had a total area of 30 m × 30 m and an inner plot of 18 m × 18 m with two buffer rows (Fig. 1). The treatments were as follows:

- (1) T1: 100A – *A. mangium* planted at a spacing of 3 m × 3 m without N fertilization;
- (2) T2: 100E – *E. grandis* planted at a spacing of 3 m × 3 m without N fertilization;
- (3) T3: 100E+N – *E. grandis* planted at a spacing of 3 m × 3 m with applications of 120 kg ha⁻¹ N;
- (4) T4: 25A:100E – *E. grandis* planted at a spacing of 3 m × 3 m, with *A. mangium* planted at a density 25% of the *E. grandis* density;
- (5) T5: 50A:100E – *E. grandis* planted at a spacing of 3 m × 3 m, and *A. mangium* planted at a density 50% of the *E. grandis* density;
- (6) T6: 100A:100E – *E. grandis* planted at a spacing of 3 m × 3 m, and *A. mangium* planted at a density 100% of the *E. grandis* density;
- (7) T7: 50A:50E – 1:1 mixture of *E. grandis* and *A. mangium* (555 trees per hectare of each species) without N fertilization.

Seedlings were planted between the rows of the previous plantation after the soil was cultivated with a ripping tyne to a 40 cm depth. *A. mangium* seedlings were inoculated with *Rhizobium* strains, and they exhibited high levels of nodulation in the nursery. In the 50A:50E treatment, the two species were planted alternately in rows and between adjacent rows (Fig. 1). *A. mangium* seedlings were planted at mid-distance between *E. grandis* trees in the same planting rows in the 25A:100E, 50A:100E and 100A:100E treatments to avoid modifying accessibility in the stand. Fertilizer inputs were representative of those used in commercial silviculture in the study region, and previous experiments showed that they did not limit tree growth. Dolomitic limestone was applied at 2 Mg ha⁻¹ at planting, and 40 g plant⁻¹ of P was buried 20 cm from the plants, as well as 9 g plant⁻¹ of K, 3 g plant⁻¹ of B, 6 g plant⁻¹ of Fe, 3 g plant⁻¹ of Zn, and 1 g plant⁻¹ of Mn. Fertilizer was applied at a rate of 25 kg ha⁻¹ of K in all treatments at 6, 12 and 18 months after planting. The main treatments were also applied to approximately 10 buffer rows on either side of each block, allowing for sequential destructive samplings without disturbing the stand growth inside the trial area. However, the number of trees was insufficient, and we had to sample several trees in block 4 at the end of the rotation.

2.2. MAESTRA model description

The MAESTRA model (Medlyn, 2004) has a long history of development and has been used to analyze diverse forest types (see the

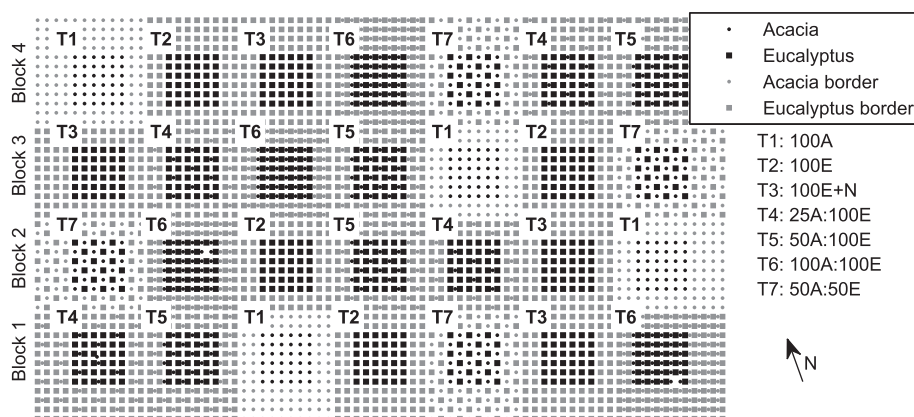


Fig. 1. Scheme of the trial. Each tree's position, including those in the borders, is represented. The treatment numbers are labeled T1 to T7, and the mixing of *Acacia* (A) and *Eucalyptus* (E) densities is given on the right side. The "+N" refers to N fertilization applied at planting and at 6, 12 and 18 months of age ($120 \text{ kg ha}^{-1} \text{ N}$ in total). The total dimension of the trial area is $220 \times 130 \text{ m}$.

bibliography at <http://www.bio.mq.edu.au/maestra/bibliog.htm>. Based on the MAESTRO model (Wang and Jarvis, 1990), MAESTRA is a 3D single-tree-based model that calculates light interception and distribution within tree crowns and uses a leaf physiology model to estimate photosynthesis, respiration and transpiration. In this study, we focus on the submodel which computes the absorbed photosynthetically active radiation (APAR) at the tree scale. The 3D model for calculating APAR is based on a study by Norman and Welles (1983) and is described in other studies (e.g., Wang and Jarvis, 1990; Medlyn, 1998; Bauerle et al., 2004).

MAESTRA represents the canopy as an array of 3D tree crowns in various simplified shapes (spherical crown, ellipsoidal, etc.). The positions, dimensions and total leaf area of each tree in the stand are inputs in the model. MAESTRA can consider different species within the stand using specific shapes and properties; however, the multi-species model has not yet been applied to our knowledge. The APAR is calculated for specified trees in the stand by taking into account the neighboring trees, which compete for light. The crown is divided in a 3D grid point with a given number of horizontal layers and a given number of points per layers. For each point in the grid, the leaf area density and the area fractions of leaves' inclination are calculated using normalized beta-distributions. Leaf transmittance and reflectance of PAR are defined for the trees as well as soil reflectance.

Single-tree APAR is calculated using the incoming radiation flux density above the canopy every half-hour and is divided into values of direct beam and diffuse radiation. If the input incident PAR is available at a daily time-step, as was the case in this study, it is converted into half-hourly PAR values using cosine functions and the sun's position. If the direct beam fraction of PAR is unknown, as in this study, it is estimated using the equations of Spitters et al. (1986).

For each grid point within the crown, the model calculates the sunlit and shaded fractions of leaf area and the flux density incident of each fraction. Multiple scattering inside tree crowns and the penetration of radiation to each grid point is calculated by the method of Norman and Welles (1983). Beer's Law is applied for both direct and diffuse radiation intercepted by a grid point. Finally, daily APAR per tree is calculated by summing the values of its grid points simulated over the course of the day.

2.3. Measurements for MAESTRA model parameterization

Three types of measurements were carried out: (i) inventories every 6 months on all of the trees in the inner plots, (ii) successive destructive samplings, used to develop relationships between the

inventory measurements and specific tree-scale characteristics, and (iii) punctual measurements made with a low frequency; for example, leaf angles or leaf optical properties.

2.3.1. Inventories: tree height and diameters

Complete inventories of all plots of the experiments, not including the borders, were performed at ages 6, 12, 18, 24, 30, 36, 41, 48, 54, 61, 66 and 72 months before harvest. These inventories were carried out by measuring the tree height, crown diameter in the row and inter-row directions (at ages 6 and 12 months for both species and at age 18 months for *Acacia* only) as well as the trunk circumference at breast height (at 18 months and older), which was converted into trunk diameter (DBH). Most of the acacias were multi-stem trees: we measured the circumference of all of the stems with a diameter at breast height (D) $> 2 \text{ cm}$. For these trees, the basal area at breast height of all the stems was collected, and an "equivalent DBH" for a single stem was calculated from the sum of the basal areas of the tree.

2.3.2. Stem and leaf biomasses, crown dimensions

Stem biomass (stem wood and bark dry weight), leaf biomass, crown length, and crown radius in both directions (i.e., row and inter-row) were estimated using allometric relationships. These allometric relationships were established at 6 months of age in the 100A and 100E treatments, using 6 trees per treatment sampled over the range of height; and at 12, 18, 30, 54 and 72 months of age for the 100A, 100E, 50A:100E and 50A:50E treatments, using 6, 8, 10, 10 and 10 trees of each species sampled in each treatment, respectively. The allometric relationships between stem biomass or leaf biomass and the inventory-related characteristics (e.g., D^2H , the product of the squared trunk diameter and tree height) were described in Laclau et al. (2008). Note that all biomass values reported in this study refer to dry mass. Likewise, allometric relationships were calibrated for crown length (defined as the distance between the bottom and top leaf of the tree) and for crown radius in the row and inter-row directions. These allometric relationships were accurate for stem biomass ($R^2 > 0.95$, except in very young stands) but were more scattered for crown radius and crown length. The allometric relationships developed in 50A:100E were used for the 25A:100E, 50A:100E and 100A:100E treatments (Laclau et al., 2008). The treatment-specific allometric relationships established at 6, 12 and 18 months of age were applied to the inventories made at the same ages. The relationships established at 30, 54 and 72 months of age were applied to the inventories made from 24 to 41 months, 48 to 61 months, and 66 to 72 months, respectively. Linear interpolations of stem biomass,

crown length and crown radius at daily time-steps are possible due to their smooth and regular evolution. However, more calculations were necessary to properly take into account the time-course of the tree leaf areas throughout the rotation.

2.3.3. Tree leaf area

From 6 to 41 months after planting, the time-course of the leaf area (LA) of each tree in the experiment was calculated from leaf biomass estimations (see section above) and the age-dependent specific leaf area (SLA). Age-dependent eucalypt SLA values were obtained from le Maire et al. (2011b) and from a new rotation in the same experiment started in 2009 (Laclau, unpublished data). From age of 48 months onwards, we directly calibrated an allometric relationship for tree LA, as described in Nouvellon et al. (2010). Because tree LA varies significantly during the year (decreasing in the dry season and increasing during the rainy season), it was not possible to linearly interpolate the leaf area estimated at each inventory date. To overcome this issue, we used the leaf area index (LAI, the surface of green leaves per surface of soil) dynamic obtained from a time-series of satellite images from a nearby *Eucalyptus* plantation, where the trees were planted at the same date as those in our study (le Maire et al., 2011a; le Maire et al., 2011b). These images cover the complete rotation and provide data on canopy reflectance, with reflectance in red and near-infrared bands correlating with the amount of green LA. *Acacia* trees were considered to follow the same LA seasonal dynamics as the *Eucalyptus*, this hypothesis being consistent with other measurements (litter-fall) and qualitative crown observations over the rotation. The interpolation procedure used between inventory dates maintained the values measured at each date and accounted for seasonal dynamics between these inventory dates.

2.3.4. Leaf angle distributions

Leaf angle distributions were measured at 12 and 64 months of age. Six trees of different sizes per treatment were selected in the 100A and 100E treatments, three trees of each species in the 50A:50E treatment were used for the 12 months measurements, and two trees of each species were used in the 50A:50E treatment for the 64 months measurements. On each tree, 72 leaves were selected as follows: at three heights in the canopy, four axillary branches were randomly selected among the four azimuthal quarters, two of them in the row direction and the other two in the inter-row direction. Six leaves were randomly selected from the area between the bottom and the end of each branch. On each leaf, the vertical component of the leaf blade's inclination was measured with a clinometer. The leaf angle distribution (LAD) was obtained at 10° intervals from the data for each species and treatment and was fitted with a Campbell function (Campbell, 1990). No difference in leaf angle distribution was observed between the treatments at 12 months of age, but differences were found between the species at 12 and 64 months of age. For *Eucalyptus*, the leaves were slightly more pendulous at 64 months than at 12 months, while the differences between the two ages for *Acacia* were not significant. For the sake of simplicity, the leaf angle distribution was considered stable across the seasons, ages and tree sizes as well as fixed to the values measured at 64 months (Table 1).

2.3.5. Leaf area density

The MAESTRA model calculates the leaf area density as the product of two beta distributions, one for the vertical direction and the other for the horizontal direction (Wang et al., 1990). Beta distributions each have three parameters that need to be calibrated. The leaf area of the top, middle and bottom parts of the crown were measured during the successive destructive samplings of leaf area, as presented above. From these three leaf area measurements per sampled tree, it was possible to compute the three

parameters of the vertical beta distribution. Different beta distributions were found for *Acacia* and *Eucalyptus* trees. For the sake of simplicity, these distributions were retained for all tree sizes or ages (Table 1). The horizontal beta distribution was measured for eucalyptus in an adjacent experiment with the same seedlings and for different ages. We measured the distance between the trunk and the leaves within the three “slices of canopy” (i.e., a quarter of the azimuth in the row or inter-row direction at 50 cm-high layers) at the bottom, middle and top of the crown. Considering that the leaves have approximately the same size as those slices, the number of leaves as a function of the distance to the trunk was plotted, and the beta distribution was adjusted. For *Acacia* trees, the horizontal distribution of leaf area density was considered to be homogeneous in accordance with our qualitative observations (Table 1).

2.3.6. Leaf and soil optical properties

We measured the optical properties of *Acacia* and *Eucalyptus* leaves at 12 months, using the same sampling design that was employed for leaf angle distributions. The reflectance and transmittance of leaves were estimated in the visible and near infrared spectra with an ASD FieldSpec Pro (Analytical Spectral Devices, Boulder, Colorado, USA) spectrometer and an ASD leaf-clip probe. The measurements were taken on a white and a black background and on the adaxial or abaxial side of the leaves. The calculations accounted for multiple scattering between the leaf and the white or black background and considered that the abaxial and adaxial transmittance should be roughly equal. The reflectance and transmittance of leaves were considered to be species-dependent; i.e., the optical properties of leaves did not vary between the trees, treatments and times (Table 1). The soil reflectance was measured directly in the field using the ASD and a white reference panel (Labsphere Inc., Sutton, NH, USA).

2.3.7. Case of border trees

The circumferences of all border trees located around each plot and around the entire experiment were measured at 61 months of age. We used regressions calibrated for each plot between the tree DBH at 61 months and DBH at the other inventory dates to extrapolate the DBH of border trees to other ages. The height of the border trees was obtained from the allometric relationships between DBH and H that were calculated on the same plot and date for each species. Once DBH and H were obtained for each border tree, the stem and leaf biomass, crown dimensions and leaf area were calculated for the trees in the treatment plots (see above).

2.3.8. Tree positions and shape

Each tree was located in a precise position in a unique scene covering the entire experiment (Fig. 1). Tree dimensions were interpolated daily as a MAESTRA model input, resulting in more than 2000 successive scenes (one of these scenes is represented in Fig. 2). *Acacia* and *Eucalyptus* crowns were represented as half-ellipsoids. The experiment was located in a field surrounded by open areas, and, together with the presence of the border trees, this provided realistic hemispherical incoming radiation simulations for each plot (i.e., no border effect). The results for block 4 were not analyzed, but this block was re-created in the simulation because it was located at the north of the experiment and therefore may significantly affect the incoming beam radiation on blocks 1–3.

2.4. Simulations and analysis of the results

A summary of the main MAESTRA parameters was listed in Table 1, and these may be different for *Eucalyptus* and *Acacia*. These parameters were kept constant for the entire rotation. Simulations were performed from the planting date (May 5th, 2003) until the

Table 1

Parameters of the MAESTRA model for absorbed photosynthetically active radiation (APAR) simulations of *Eucalyptus grandis* (E) and *Acacia mangium* (A) species. For the sake of clarity, the variable names were kept exactly as in MAESTRA source code and manual (<http://www.bio.mq.edu.au/maestra/manual.htm>), and the arrays of values are given in the same order.

Species	Parameter name and definition	Value
E and A	lat: latitude	23°2'28.8"S
E and A	long: longitude	48°37'34"W
E and A	notrees: number of surrounding trees	500
E and A	nolay, pplay, nzen, naz: number of angles and layers to integrate over	6, 12, 5, 11 (default)
E and A	difsky: distribution of diffuse radiation incident from the sky	0 (uniform sky)
E and A	khersperday: number of timesteps per day	48
E	rhosol: soil reflectance in PAR ^a , NIR ^b and thermal	0.067, 0.270, 0.05
E	atau: leaf transmittance in PAR, NIR and thermal	0.034, 0.328, 0.01
E	arho: leaf reflectance in PAR, NIR and thermal	0.048, 0.247, 0.05
A	rhosol: soil reflectance in PAR, NIR and thermal	0.067, 0.270, 0.05
A	atau: leaf transmittance in PAR, NIR and thermal	0.063, 0.296, 0.01
A	arho: leaf reflectance in PAR, NIR and thermal	0.074, 0.206, 0.05
E and A	cshape: crown shape	ELIP (half-ellipsoidal)
E and A	nalpha: number of leaf angle classes from 0° to 90°	9
E	falpha: proportion of leaf area in each angle class.	0.007, 0.022, 0.041, 0.064, 0.094, 0.132, 0.176, 0.219, 0.245
A	falpha: proportion of leaf area in each angle class	0.053, 0.130, 0.156, 0.148, 0.129, 0.111, 0.098, 0.090, 0.086
E	bpt: beta dist. parameters for the vertical and horizontal leaf area density	5.707, 1.296, 0.711, 2.280, 1.218, 1.048
A	bpt: beta dist. parameters for the vertical and horizontal leaf area density	2.825, 0.840, 0.340, 0.0, 0.0, 0.0

^a Photosynthetically active radiation.

^b Near infrared.

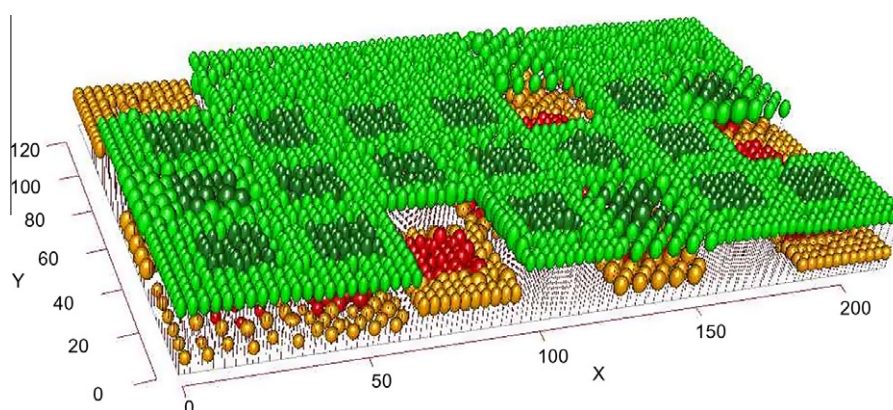


Fig. 2. Representation of the trial at 54 months, which is an input of the MAESTRA model and shows *Eucalyptus* dominating the *Acacia* trees. Absorbed photosynthetically active radiation (APAR) was calculated for each *Eucalyptus* tree (in dark green) and *Acacia* tree (in red). *Eucalyptus* trees represented in light green and *Acacia* trees in orange are either border trees or belong to Block number 4. X and Y are measured in meters (refer to Fig. 1 for the orientation). This figure was created with the R package Maeswrap (R. Duursma, <http://cran.r-project.org/web/packages/Maeswrap/index.html>). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

last inventory at age 72 months (May 5th, 2009) prior to harvesting. The daily global radiation used for this period was recorded at the UNESP station in Botucatu (SP, Brazil), which was 30 km away from the Itatinga experimental site. Simulations were done at half-hour time-steps. For each tree, the closest 500 surrounding trees were considered when calculating the light reaching that tree's crown. Due to the large number of trees and length of time required for the simulations, the simulations were done on a cluster of computers. The primary output that we analyzed was the daily absorbed PAR for each tree in each plot of blocks 1–3. To analyze inter-tree variability among the same plot, APAR values were cumulated for the entire rotation and compared to the stem biomass increment. To analyze the differences between the treatments and the effect of mixing acacias with eucalypts, the sum of the APAR of all trees within a given plot was divided by the area of that plot. This indicated the amount of light absorbed by ground area units and allowed for the comparison between the plots. Annual sums of APAR values were calculated to analyze their variation as a function of stand age and were compared to the annual increments in stem biomass. The differences among the treatments

and blocks for several variables were tested with SAS 9.1 using a two-way ANOVA. The homogeneity of variances was assessed using Levene's test, and the original values were transformed when variances were unequal. The probability level used to determine significance was $P < 0.05$. When significant differences between treatment levels were detected, Bonferroni's multiple range test was used to compare the treatment methods.

The biomass of the tree stem increment (ΔB_s , in grams of dry matter per year at tree scale [g year^{-1}]) was decomposed to study the effect of tree leaf area (LA, m^2), PAR absorption efficiency ($\Phi_{\text{area}} = \text{APAR}/\text{LA}$, $\text{MJ year}^{-1} \text{m}^{-2}$) and light use efficiency ($\text{LUE} = \Delta B_s/\text{APAR}$, g MJ^{-1})

$$\Delta B_s = \text{LA} \times \Phi_{\text{area}} \times \text{LUE} \quad (1)$$

The LUE could be decomposed into several factors based on a widely used LUE model (McMurtrie et al., 1994; Landsberg and Waring, 1997) applied at an annual time-step:

$$\text{LUE} = \frac{\Delta B_s}{\text{APAR}} = \varepsilon_{\text{max}} \times f_c(c) \times f_w(w) \times f_n(n) \times f_a(a), \quad (2)$$

where ε_{\max} is the maximum potential LUE (gMJ^{-1}) for net primary production, i.e., for optimal climatic conditions and in the absence of soil water and nutrient limitations. $f_c(c)$, $f_w(w)$ and $f_n(n)$ are limiting factors of the range 0–1 that are functions of climate (e.g., vapor pressure deficit, temperature), soil water content and nutrients, respectively. The function $f_a(a)$ represents the fraction of the primary productivity that is allocated to the stem biomass. This model implies that a change in LUE would be caused by a change in ε_{\max} or one of the limiting factors mentioned above.

2.5. Validation of the light interception

Measurements of directional gap fractions (GF) were taken with a LiCor PCA LAI-2000 (Li-Cor, Lincoln, NE, USA) at two dates (August 12th and 25th, 2008) in three treatments (100A, 100E, and 50A:50E) in blocks 1, 2 and 3 (i.e., 9 plots). In each plot, 32 measurements were taken below the canopy with a LAI-2000 device using a 90° azimuthal field of view that was oriented toward the north in 100% diffuse light conditions. The locations of the measurements were chosen on a systematic grid to cover the central part of the plot and to sample points at different distances from the trees (but never in front of a tree trunk). Continuous measurements of incident radiation were performed simultaneously in an adjacent open area with a second LAI-2000 inter-calibrated with the first one and used with the same measurement configuration (oriented toward the north and with a view cap allowing for a 90° azimuthal field of view). The ratio between below- and above-canopy (incident) radiations was calculated for the different zenithal rings of the LAI-2000 fish eye and provided an estimate of the directional gap fraction. These measured GF were used to test the MAESTRA simulations. We simulated the GF at the locations and angles where LAI-2000 measurements were performed using the MAESTRA scene for the same date, with the leaf reflectance and transmittance values set close to 0. The LAI-2000 has an optical filter that detects light below 490 nm, which is a value at which foliage reflects and transmits relatively little radiation (LAI-2000 manual). The simulated and measured angular GF values were then averaged per treatment and compared.

3. Results

3.1. Validation of the light interception

The simulated and measured gap fractions were averaged by treatment group for the three first angles and displayed a good agreement (Fig. 3). Gap fractions were slightly over-estimated for all angles in the 100A and 100E treatments and were underestimated in the 50A:50E treatment. This led to an under-estimation of the intercepted light (averaged over the 3 angles and 2 dates) of 3.4% for 100A, 4.5% for 100E and an over-estimation of about 4.6% for 50A:50E. Despite these small biases, the simulations correctly represented the changes in the zenithal angle and date as well as the large difference between the two species.

3.2. Stand-scale APAR and light use efficiency

3.2.1. Monospecific stands

The LAI values averaged over the full rotation were significantly higher in the monospecific *Eucalyptus* stands than in the *Acacia* stands (Table 2). This pattern was directly reflected in the APAR values, where *Acacia* absorbed 24% less radiation than *Eucalyptus* over the rotation. The stem (wood and bark) growth was much higher for the monospecific stands of *Eucalyptus* than for *Acacia*. At 6 years of age, the stem biomass in the 100A treatment was only 60% of that in 100E with the same stocking density. The differences

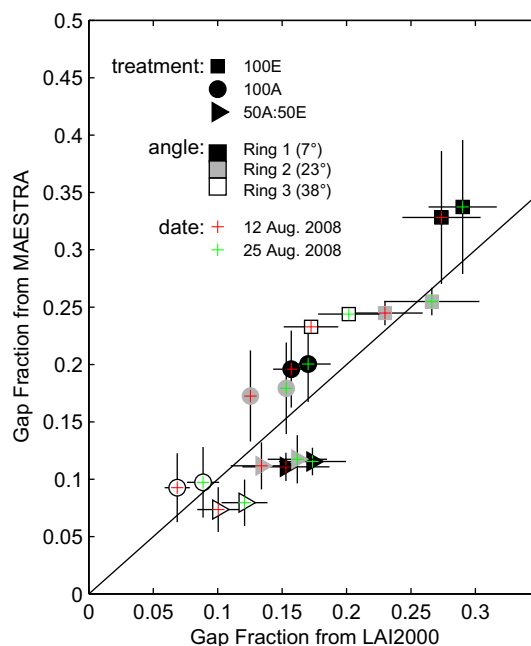


Fig. 3. Comparison of gap fractions measured on the three first rings of a LAI-2000 device (black, grey and white symbols, respectively) with predictions from the MAESTRA simulations for the two monospecific treatments (100E, squares; 100A, circles) and the other treatment of the replacement series (50A:50E, triangles). The measurements were taken at two different dates in 2008 (colored crosses).

between 100E and 100E+N were low and not significant in terms of absorbed radiation and stem growth, and this finding was also observed by Laclau et al. (2008). Therefore, our study did not differentiate between these two treatments, and only the 100E treatment was retained for analysis. Note that the inter-block variability in APAR and stem growth was low, with coefficients of variations <5%.

The mean LUE values were significantly higher in the 100E treatment (around 1.05 g MJ^{-1}) than in the 100A group (0.87 g MJ^{-1}). Therefore, for the same amount of radiation absorbed by the canopy, the *Eucalyptus* trees produced 20% more stem biomass than the *Acacia* trees in monospecific stands (Table 2).

3.2.2. Effects of mixing *Acacia* and *Eucalyptus* trees on LUE

The additive and replacement experiment designs provided complementary information on *Eucalyptus* and *Acacia* plasticity, both in terms of LAI and APAR. In the additive series, total stand LAI increased with the density of *Acacia* trees in response to the rise in *Acacia* LAI, which was nearly proportional to the density of this species. *Eucalyptus* LAI remained unchanged (Table 2). This pattern also occurred for the average absorbed PAR throughout the rotation. The differences in mean LAI that occurred over the rotation explained most of the variation in the APAR of *Acacia* trees. However, the APAR/LAI ratio of *Acacia* trees in the additive series was higher than that of *Acacia* trees in the monospecific stands due to lower LAI. The total LAI of the 50A:50E stand was 12% higher than the LAI of the 100E stand and was 20% higher than the sum of half the LAI of the 100A and 100E stands. *Eucalyptus* in the 50A:50E stand had a high average LAI (2.67), whereas *Acacia* trees in this stand had a low LAI (1.15) when compared to the monospecific stand values.

In the additive series, the *Eucalyptus* absorbed a large part of the incoming PAR compared to *Acacia*. In the replacement plots, the *Eucalyptus* also absorbed a large part of the radiation, even when it was planted at half-density. To compare the effect of mixing on a given species, it was necessary to use variable values

Table 2

Leaf area index (LAI), absorbed photosynthetically active radiation (APAR), stem biomass growth (ΔB_s), and light use efficiency for stem production (LUE, the ratio of stem growth to APAR) averaged over the six years of the rotation, together with the standard deviation between blocks (std) for *Eucalyptus grandis* (E) and *Acacia mangium* (A). APAR was computed with the MAESTRA-simulated value for each tree, summed over the plot, and divided by the plot area. Stem growth and LAI were measured. Test 1 and Test 2 used Bonferroni's *t*-test to group the treatment that had mean values not significantly different (same letter) with a probability alpha = 0.05. Test 1 compared the stand values, whereas Test 2 compared the *Eucalyptus* trees in the additive series.

Treatment	Species	LAI				APAR (MJm ⁻² year ⁻¹)				ΔB_s (gm ⁻² year ⁻¹)				LUE (gMJ ⁻¹)			
		Mean	Std	Test 1	Test 2	Mean	Std	Test 1	Test 2	Mean	Std	Test 1	Test 2	Mean	Std	Test 1	Test 2
100A	A	3.00	0.20	e		1472	60	e		1278	148	c		0.87	0.07	b,c	
100E	E	3.40	0.08	d	b	1949	30	d	a,b	2043	73	a	a,b	1.05	0.05	a	a,b
100E+N	E	3.80	0.07	b,c	a	2050	12	c,d	a	2150	82	a	a	1.05	0.03	a	a,b
25A:100E	E	3.32	0.07		b	1941	45		a,b	2074	64		a,b	1.07	0.03		a
	A	0.20	0.06			147	33			42	13			0.28	0.03		
	A+E	3.52	0.04	c,d		2088	46	b,c,d		2115	52	a		1.01	0.03	a	
50A:100E	E	3.20	0.06		b	1903	11		b	1946	86		a,b	1.02	0.05		a,b
	A	0.46	0.03			321	22			95	9			0.29	0.01		
	A+E	3.66	0.09	b,c,d		2225	25	b		2040	93	a		0.92	0.04	b	
100A:100E	E	3.16	0.11		b	1890	59		b	1846	121		b	0.98	0.04		b
	A	0.91	0.12			616	26			165	23			0.27	0.03		
	A+E	4.07	0.01	a		2506	33	a		2011	101	a		0.80	0.03	c	
50A:50E	E	2.67	0.23			1644	135			1377	132			0.84	0.03		
	A	1.15	0.14			501	48			302	23			0.60	0.02		
	A+E	3.82	0.09	a,b		2145	95	b,c		1678	113	b		0.78	0.02	c	

expressed at tree scale (dividing the stand values in Table 2 by the number of trees). For instance, the *Acacia* trees in the mixed 50A:50E plots have an APAR that was only 68% of the value measured in monospecific *Acacia* stands. On the contrary, the APAR of *Eucalyptus* at tree scale was 169% of the value in 100E. The total APAR in the mixed species plots was higher than in the pure plots, showing that the mixed plots captured the light better.

The stem growth of an average *Acacia* tree in the additive design was lower than that measured in the pure stands (Table 2). In the 100A:100E plot, the ΔB_s of *Acacia* averaged over the rotation was only 13% of the value measured in the monospecific *Acacia* stands. On the contrary, the ΔB_s of *Eucalyptus* trees was as high in the 25A:100E, 50A:100E and 100A:100E treatments as in the 100E treatment (Table 2, significance Test 2). The total production of stem biomass per plot was therefore almost constant regardless of the *Acacias*' density. In the replacement design, the ΔB_s of an average *Eucalyptus* tree (dividing the area based values of Table 2 by the number of trees) was 1.3 times higher than in a pure stand, and for *Acacia*, it was 0.47 times lower. This finding implies that *Eucalyptus* improved its productivity and that *Acacia* lost productivity in the 50A:50E mixed stand. Competition between *Acacia* trees and *Eucalyptus* trees was therefore lower than in the intra-specific competition of the 100E stand, and the competition between *Eucalyptus* and *Acacia* was higher than in the intra-specific competition of the 100A plot. The ratio of total stem growth in the 50A:50E mixture divided by the average stem growth in the pure stands of the 100A and 100E treatments was close to 1. Therefore, mixing the *Eucalyptus* and *Acacia* trees in the 50A:50E treatment did not benefit the system.

The inter-specific dominance of *Eucalyptus* trees in the 50A:50E plot strongly enhanced their stem growth and APAR in comparison with the 100E treatment. The ratio between stem growth and APAR (i.e., the LUE) was also different between the treatments, showing that the differences in growth between the stands were due to the quantity of radiation absorbed by the trees (see Eq. (2)). For instance, *Acacia* absorbed less light in the additive series than in the monospecific plots because they were dominated by *Eucalyptus*. But on top of that, for the same amount of light absorbed, *Acacia* produced less stemwood: the LUE of *Acacia* was reduced by 70% in the 100A:100E stand compared to that reported in the monoculture. In the 50A:50E plot, the *Acacia* LUE was reduced by 31% compared with 100A. The LUE of *Eucalyptus* trees steadily decreased with increasing densities of *Acacia* trees. In the

50A:50E plot, the LUE of *Eucalyptus* trees was reduced by 20% compared to that measured in the monospecific plots. The total LUE of the 50A:100E and 100A:100E mixtures (i.e., a stand's stem growth divided by its APAR) were significantly smaller than the LUE of the pure *Eucalyptus* stands (Table 2, significance test 1).

3.2.3. LUE variations with tree age

The LAI, APAR, stem growth and LUE values changed with age in the experiment (Fig. 4). The changes in LUE with age were a consequence of changes in APAR and productivity. These variations resulted from the inter-annual variability in climate as well as changes in a tree's functioning with age (Eq. (2)). The LUE of the 100E stand increased with age until stabilizing at 4 years of age, while the LUE of the 100A stand decreased between 2 and 4 years of age and increased between the two last years of the rotation. The LUE of *Acacia* and *Eucalyptus* in the 50A:50E plot matched the LUE of monospecific stands over the first 4 years, and they both decreased in the 5th and 6th years (reduction of about 30% in LUE). The LUE of *Acacia* reduced noticeably with age in the additive treatments, showing a completely different shape than that in the monospecific *Acacia* stands. The differences in the LUE of *Acacia* between the treatments in the additive series were not significant. The error in these LUE estimates may be large due to the small values of annual APAR and stem growth. The LUE of *Eucalyptus* in the additive series remained nearly stable from 2 to 5 years of age and decreased during the 6th year in the 25A:100E, 50A:100E, and 100A:100E treatments. At 6 years of age, the LUE values of these groups were significantly lower than that of the 100E treatment.

3.3. Tree-scale APAR and light use efficiency

3.3.1. Monospecific stands

The tree leaf area, APAR and stem growth were non-linearly correlated with tree size (Fig. 5). In both *Eucalyptus* and *Acacia*, the tall trees absorbed disproportionately more light and grew faster than the small trees, i.e., there was an intra-specific and size-asymmetric competition for light.

The link between tree size and tree growth was decomposed based on Eq. (1) (Fig. 5) to test for the significance of each variable with tree height. In the 100A treatment, tall trees: (1) had a larger leaf area (LA), and (2) produced more stem biomass per unit of leaf area (i.e., higher growth efficiency [GE]). This occurred because these trees absorbed approximately the same amount of PAR per

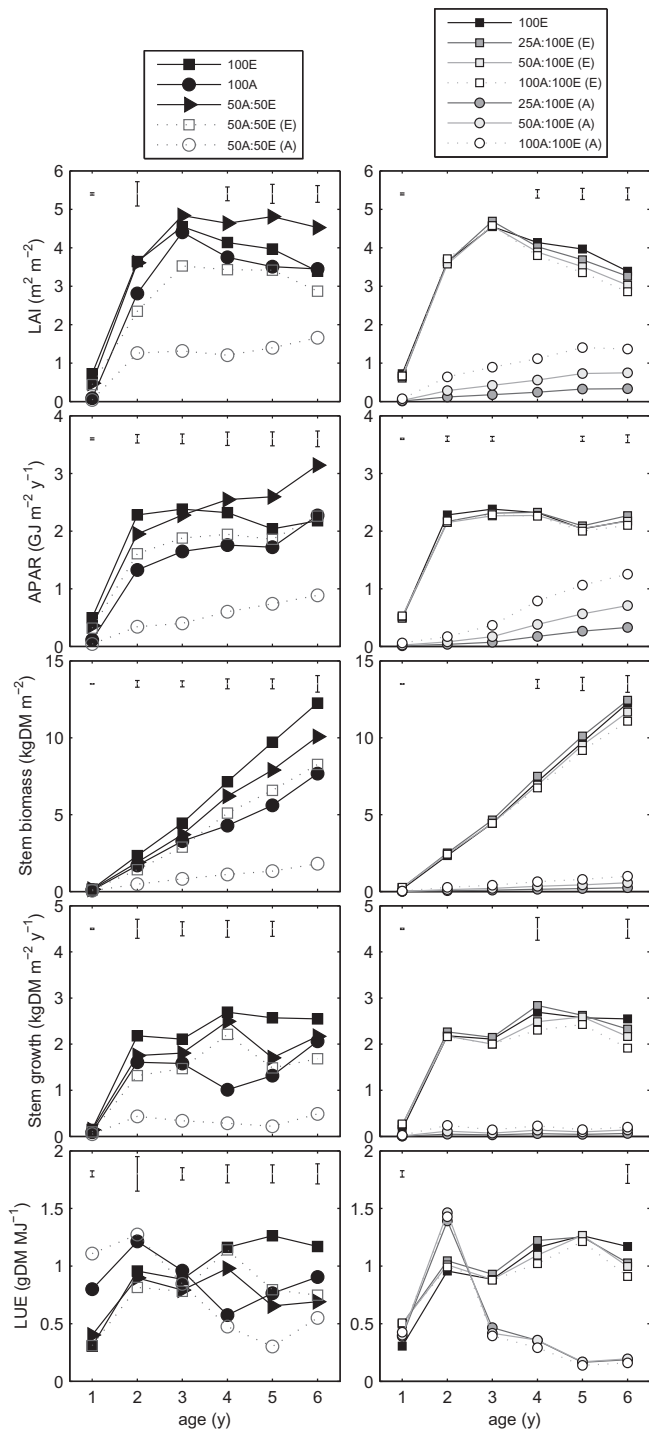


Fig. 4. Annual variations of leaf area index (LAI), absorbed photosynthetically active radiation (APAR), stem biomass, stem growth and light use efficiency for stem production on all treatments of the experiment. When the two species are mixed, the E in brackets stands for the *Eucalyptus* trees in that treatment (A for *Acacia*). Vertical bars indicate the least significant difference (LSD) at each age. LSD is only represented when treatments are significantly different. In the replacement series (on the left), LSDs are computed for the whole stand values, and in the additive series (on the right), LSDs are computed for the *Eucalyptus* trees only.

unit of leaf area (Φ_{area}) but produced more stem biomass per unit of absorbed PAR (LUE). This decomposition suggested that the big trees could produce more stem biomass not only because they had more leaf area (to capture light) but also because they were more efficient at converting the absorbed PAR into stem biomass.

In the 100E treatment, the tall trees: (1) had a larger leaf area and (2) produced more stem biomass per unit of leaf area than the short trees. This result occurred because the tall trees in this stand absorbed more PAR per unit of leaf area and also produced almost the same stem biomass per unit of absorbed PAR (except in the case of the very small trees). This decomposition suggested that the big trees could produce more stem biomass because they had more leaf area and were more efficient in capturing light than the short trees.

3.3.2. Mixed-species stands

Acacia displayed the same pattern of function for tree height in both the 50A:50E and 100A treatments (Fig. 5). *Eucalyptus* trees in the 50A:50E stand presented a slightly different pattern of functioning than those in the 100E stand. Tall *Eucalyptus* trees: (1) had a bigger leaf area but (2) produced almost the same stem biomass per unit of leaf area as the smaller *Eucalyptus* trees. This result occurred because they absorbed almost the same PAR per unit of leaf area, and they produced almost the same stem biomass per unit of absorbed PAR. The increase in stem production with tree height was due to the increase in the tree leaf area and the corresponding APAR.

Inter-specific interactions led to the reduction of the average LUE in both *Acacia* and *Eucalyptus*. However, the trends observed in mono-specific stands still applied, particularly in regard to an increase in LUE with tree height observed in *Acacia* but not in *Eucalyptus*. The individual size of *Eucalyptus* trees increased in comparison to the 100E treatment, and the presence of *Acacia* in the understory seemed to reduce the *Eucalyptus* access to below-ground resources slightly, and/or changed the allocation pattern independently of their size (Eq. (2)).

4. Discussion

4.1. Use of models to estimate APAR

Several studies have used 3D models to analyze intra-species competition for light (e.g., Binkley et al., 2002; Bauerle et al., 2004; Binkley et al., 2009, 2010). In this study, we used a 3D model to isolate the effects of intra- and inter-specific competition for light from other processes. This modeling approach is complementary to other types of research that study the functioning of mixed-species plantations, reported by Kelty (2006). The tree-scale APAR is an important variable as it provides insight into the mechanisms that influence stand productivity or at least disentangles the effect of light absorption from other potential causes. As APAR is not directly measurable at the tree scale in closed canopies, the use of a light interception model is then required. In this study, we chose a 3D model of intermediate complexity, representing the tree as a simple geometrical form. More realistic models could have been used, such as 3D architectural models that represent each leaf, branch and trunk (Parveaud et al., 2008). However, when annual ecosystem budgets of carbon and water are analyzed, simple models may yield results similar to those from architectural models (Roupsard et al., 2008). Despite its simple geometrical representation of the tree, the MAESTRA model takes into account the following important variables: crown size and position, leaf area density distribution, leaf angle distributions, and the differences in these variables between species.

The use of a model requires a comprehensive parameterization and a validation from an independent dataset. In this study, most of the parameters were measured in situ. However, some structural variables were kept constant during the rotation and for all tree sizes. These variables, such as the leaf angle distribution, leaf reflectance, leaf density distribution or within-canopy clumping,

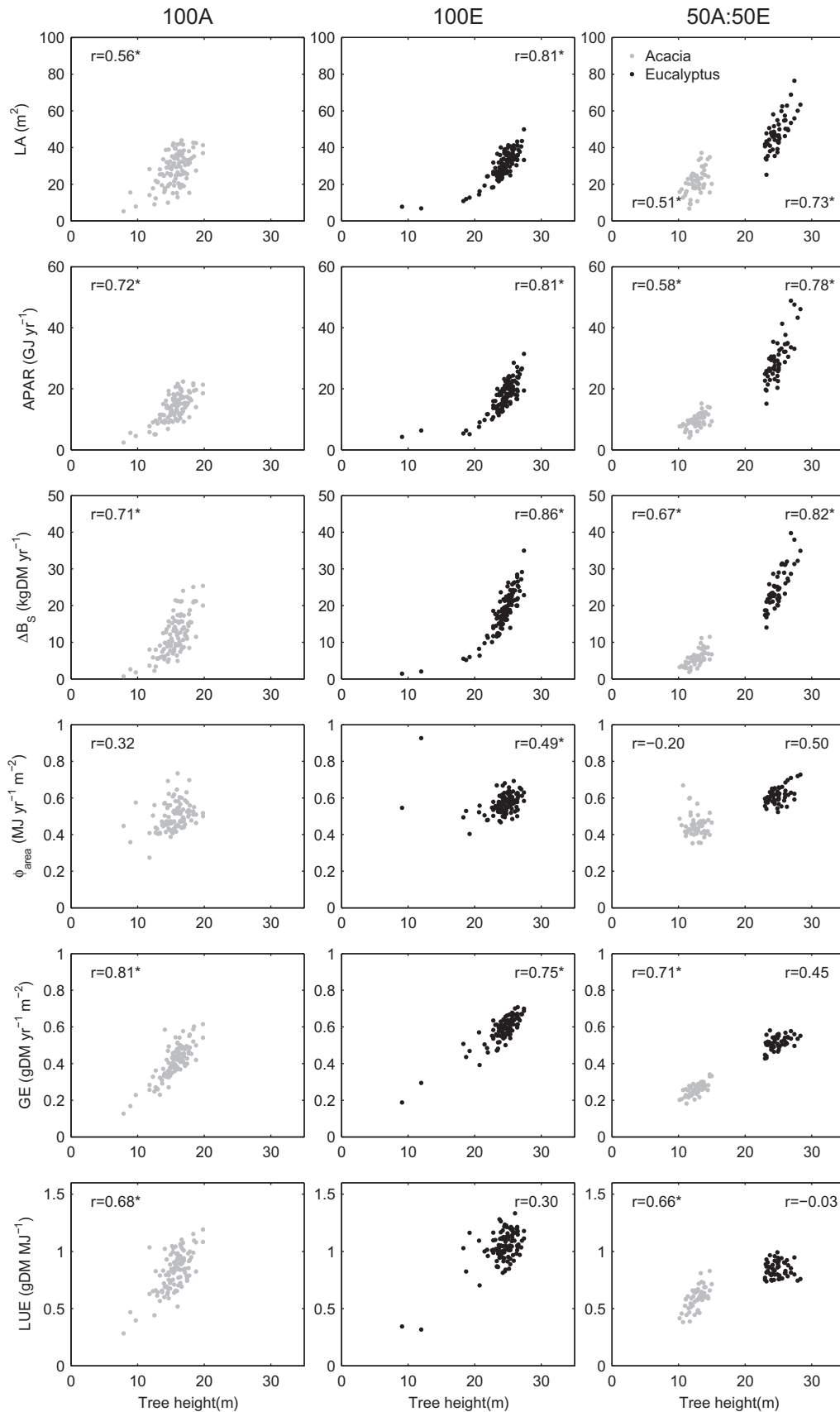


Fig. 5. Average values of tree leaf area (LA), absorbed photosynthetically active radiation (APAR) and stem growth (ΔB_s) over the whole rotation for each tree in the 100A, 100E and 50A:50E treatments as a function of tree height. Φ_{area} is the ratio of tree APAR/LA and represents the efficiency of the plant to capture light. GE is the ratio of tree growth divided by leaf area and represents the growth efficiency. LUE is the ratio of tree ΔB_s divided by APAR and represents the light use efficiency of the tree. Tree height is the height of all of the trees of each species in blocks 1, 2 and 3 at the end of the rotation (excluding 2 buffer rows). Pearson's correlation coefficient (r) is given with its significance ($*p < 0.0001$). For the 100E treatment, the two smallest trees were excluded from the r calculations.

may vary over time and due to tree size (e.g., for leaf angle distribution and reflectances: le Maire et al., 2011b) or even change between treatments. In the future, we will conduct a sensitivity analysis of the model on the structural variables for APAR simulations. This will give information about MAESTRA parameter or variable which have to be measured in situ, or on contrary that can be fixed to average values from literature, in order to simulate *Eucalyptus* and *Acacia* APAR during a full rotation.

Despite these limitations and other simplifications in the model (no light interception by branches or trunks, no inter-tree scattering, etc.), the model performed well and simulated the canopy light interception at a level of accuracy similar to our LAI2000 measurements (less than 5% difference) (Fig. 3). The simulation results also show almost linear relationships between APAR and LA at tree scale, as is often noticed in forests (Fig. 5) (Binkley et al., 2012). Note that at the end of the rotation, the average tree height of the 100A treatment was lower than other surrounding treatments for *Eucalyptus* (Fig. 2), and therefore, the APAR of the 100A plot was lower than the APAR that might be expected if this plot were surrounded by other 100A plots (not shown). One of the strengths of 3D radiative transfer models like MAESTRA is their ability to take into account not only the light interactions between the trees inside a plot but also the possible influence of open spaces or trees on neighboring plots. This feature is absent in models based on infinite homogeneous canopies, like the SAIL model (e.g., SAIL model Verhoef, 1984).

4.2. Light use efficiencies in pure and mixed-species plantations

LUE was defined in our study as the stem biomass growth divided by the amount of light absorbed and was estimated at 1.05 g MJ^{-1} on average for *Eucalyptus* monocultures. Marsden et al. (2010) reported a LUE of 1.18 g MJ^{-1} in other Brazilian *Eucalyptus* plantations on a different hybrid. Our estimate of LUE did not take into account the leaves and branches production and was therefore expected to be about 30% lower than the LUE for aboveground net primary production (ANPP) (data not shown). Considering this difference, the LUEs reported in our study were within the upper half range of *Eucalyptus* ANPP LUE reported in the literature (Binkley et al., 1992; Giardina et al., 2003; Stape et al., 2004; Whitehead and Beadle, 2004; du Toit, 2008; Stape et al., 2008). The ANPP LUE reported in these studies ranged from 0.47 g MJ^{-1} in climatic zones limited by water availability to 2 g MJ^{-1} in highly productive regions. The variations that we recorded in LUE due to tree age (reported in Fig. 4) were also comparable to those found by Marsden et al. (2010). The values of LUE were very low for the first two years after planting and then increased in years 4 and 5. The low LUE that occurs during the early growth stages could be caused by the majority of photosynthates being allocated to build resource-capturing organs (leaves and roots) therefore leading to a low value of $f_a(a)$ in Eq. (2).

Few studies have reported LUE values for pure *Acacia* plantations. In this study, we estimated the LUE value of such a stand to be, on average, 0.87 g MJ^{-1} over a 6-year rotation. This estimate is comparable to the values reported by Khasanah et al. (2006) for *A. mangium* in Indonesia (1.03 g MJ^{-1} for aboveground biomass). More interestingly, when *A. mangium* was dominated by *Hevea brasiliensis* in a mixed-species plantation, the LUE of this *Acacia* decreased to a value of 0.38 g MJ^{-1} (Khasanah et al., 2006), and this finding is comparable to the dynamic observed in our study of mixed-species plantations with *E. grandis* (0.87 g MJ^{-1} in the 100A stand and 0.28 g MJ^{-1} in the additive series).

4.3. Analysis of the variability in LUE

The canopy stratification observed from 2 years and onward led to a niche complementarity between *Acacia* and *Eucalyptus* to

capture the light resource in the mixed-species plantations. The LAI, leaf angles and crown sizes of *Eucalyptus* allowed a large amount of light to penetrate its canopy (see the high gap fractions of 100E in Fig. 3) and to be used by an understory tree stratum, as was observed in other *Eucalyptus*–*Acacia* associations (Bauhus et al., 2004). There was an increase in total APAR intercepted by the stand in the additive series, and the amount of PAR absorbed by *Acacia* in the 100A:100E plot was not negligible.

However, complementarity for light capture did not affect stem biomass production, suggesting that the differences in stem growth were not only due to different light absorption patterns. *Acacia* trees received less light in mixed-species plots, leading to less absorption and thus less growth, but there were other factors further reducing their stemwood production. These factors were likely to change with stand age (Hunt et al., 2006; Forrester et al., 2011). We can separate them into different processes, as in Eq. (2), and rely on other research studies to disentangle the relationships between these different factors.

4.3.1. Climatic factor

This factor probably played a minor role in the time-course of LUE, given that the test plots were located at the same site. Nevertheless, micro-climatic differences among trees growing in monocultures or in mix stands may occur (Rao et al., 1997). Changes in the ϵ_{max} value in Eq. (2) may also occur, as trees acclimate to their micro-environment (Misson et al., 2006; Richards et al., 2010).

4.3.2. Allocation

The allocation patterns changed for *Acacia* and *Eucalyptus* in the 50A:50E stand. In a recent study using the same experimental data, Nouvellon et al. (2012) found that 4–6 years after planting, the proportion of GPP allocated to stem production was significantly lower in the 50A:50E treatment (for both species) than in the 100A and 100E treatments. Moreover, the proportions of GPP allocated for belowground and for aboveground litter production were higher in the 50A:50E treatment than in the A100 and E100 treatment. The total biomass of fine roots was also higher in the 50A:50E plot at 5 years of age (Laclau et al., submitted), which resulted from an increase in the fine roots of *Eucalyptus* in comparison to the levels in the 100E treatment. Therefore, these results suggest that the lower light use efficiencies in stem production of *Acacia* and *Eucalyptus* trees in the mixed 50A:50E plot partly resulted from shifts in carbon partitioning. Partitioning was directed towards the production of resource-capturing organs (leaves, branches and roots) and away from stemwood production. The changes towards the resource-capturing organs in the carbon partitioning of *Acacia* in the understory of the additive series were likely, as they have been reported for suppressed trees (Hunt et al., 2006), but were not quantified here.

4.3.3. Water and nutrients

Fertilization trials at our study site showed that the amounts of fertilizer applied were mostly not limiting the tree growth, with the slight exception of N in the first two years after planting (Goncalves et al., 2008; Laclau et al., 2008; Laclau et al., 2010). From two years of age onward, almost all of the available water stored in the soil after clear-cutting is taken up by *Eucalyptus* roots, and at the end of the rotation, all of the annual rainfall is evapotranspired (Nouvelon et al., 2011). Additionally, stand growth is limited by water availability in Southeast Brazil (Stape et al., 2010). The overall picture is therefore a greater water than nutrient limitation, as also corroborated by similar nutrient concentrations in tree compartments in mono-specific plots and mixtures throughout the rotation (data not shown). As a consequence, in the mixed *Acacia*–*Eucalyptus* plots, the trees with a high proportion of fine roots in the superficial soil layers (which are the only soil layers moistened during small

rainfall events) were the most able to take up water and nutrients (the latter of which were liberated during the decomposition of forest floor litter (Laclau et al., submitted)). The 50A:50E plot had almost the same *Eucalyptus* fine root biomass in the superficial horizon as the 100E plot, despite a 50% lower stocking density in the former. By contrast, the fine root distribution of *Acacia* in the 50A:50E treatment had a higher proportion of roots in deep soil layers compared to the 100A stand, and this was caused by the roots' partial exclusion in the top soil due to competition with the roots of *Eucalyptus* trees. Laclau et al. (submitted) drew a parallel between the inter-specific competition for water and nutrient resources below-ground and light resource aboveground, as all of these resources are directional and limited (Schenk, 2006; Laclau et al., submitted). The belowground competition for water between *Eucalyptus* and *Acacia* trees was therefore also likely to contribute to the decrease in the LUE of *Acacia* trees in mixed stand by reducing their photosynthetic activity (e.g., stomatal closure). The overyielding of the fine roots of *Eucalyptus* trees in the 50A:50E plot could have a significant role in the reduction of the LUE of *Eucalyptus* trees when compared with monospecific *Eucalyptus* stands (Nouvellon et al., 2012).

4.3.4. Consequences for forest management

Although stratified canopies in mixed-species forests can increase the overall capture of light, this niche complementarity that occurs aboveground may not lead to an increase in stem biomass if another important resource is strongly limiting tree growth. The decrease in LUE at the end of the rotation in the 50A:50E treatment in our study suggests that mixed-species plantations designed to maximize biomass production through a stratified canopy should be established in regions not prone to drought and with sufficient fertilizer inputs (except N, if N₂-fixing species are included in the mixture) to maintain high LUEs throughout the stand's development. However, this hypothesis has to be confirmed by experimental setups under different climatic conditions and soil fertility gradients.

5. Conclusion

This study contributed to understanding the processes involved in intra- and inter-species sharing of light resources and their relationship with stem growth. The MAESTRA model was used to simulate the light interception of a complex canopy of pure and mixed plantations consisting of two species with different structural properties. The application of this model over a full rotation made it possible to compare the amount of absorbed light with the stem growth of two species in monospecific plantations and under different proportions of mixing.

Based on the analysis of light absorption and stem growth at the tree scale in our study, and using complementary results provided by other studies on the same trial experiment (Bouillet et al., 2008; Laclau et al., 2008; Laclau et al., submitted; Nouvellon et al., 2012), we can summarize the competitive mechanisms occurring in the pure and mixed-species plantations as follows:

- Nitrogen-fixing species did not increase stem biomass production in the mixed-species plantations, and this result can be attributed to the *Eucalyptus* trees' competitive advantage in capturing the soil resources and the relative abundance of N in the soil at this site.
- The competition for resources in these highly productive plantations dominates the interactions. Replacing *Eucalyptus* trees with *Acacia* trees lead to a competitive reduction for *Eucalyptus*. Although the *Eucalyptus* trees in the replacement plots grew faster than in the pure stands, this increment did not compensate for the large reduction in *Acacia* growth.

- In the mixed-species plantations before canopy closure, *Acacia* trees allocated their assimilated carbon mainly to vertical growth in an effort to compete with *Eucalyptus* trees for light. However, *Eucalyptus* trees grew faster in height. When the *Acacia* trees were completely overcome by the *Eucalyptus* canopy (about 2 years after planting in the additive series and 3 years after planting in the replacement plots), they invested relatively more biomass on their resource-capturing organs (leaves and fine roots) and less on stemwood production, and they likely suffered from greater water stress (than in *Acacia* monocultures) due to competition with *Eucalyptus* trees.

The benefit of the association of N-fixing species with *Eucalyptus* might have occurred over a longer timescale at our study site. Moreover, it is necessary to test the associations described in this study under other climates and resource availabilities. Modeling approaches should be developed that take into account the consequences of the availability of water and nutrients on tree growth as this would clarify the effects of natural resources on intra- and inter-specific interactions.

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