Light absorption, light use efficiency and productivity of 16 contrasted genotypes of several Eucalyptus species along a 6-year rotation in Brazil

Guerric le Maire (1,2,3), guerric.le_maire@cirad.fr Joannès Guillemot (1,3,4), joannes.guillemot@cirad.fr Otavio C. Campoe (5,6), otavio.campoe@ufla.br José-Luiz Stape (6), jlstape@gmail.com Jean-Paul Laclau (1,3), laclau@cirad.fr Yann Nouvellon (1,3), yann.nouvellon@cirad.fr<br>(1) CIRAD, UMR Eco\&Sols, F-34398 Montpellier, France<br>(2) UNICAMP, Campinas, SP, CEP: 13083-860, Brazil<br>(3) Eco\&Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier, SupAgro, Montpellier, France<br>(4) ESALQ, Universidade de São Paulo, Piracicaba, SP, CEP 13418-900, Brazil<br>(5) Federal University of Lavras - UFLA, Lavras, MG, CEP: 37.200-000, Brazil<br>(6) UNESP-FCA, Botucatu, SP, CEP 18.610-300, Brazil


#### Abstract

Stemwood productivity in forest ecosystems depends on the amount of light absorbed by the trees (APAR) and on the Light Use Efficiency (LUE), i.e. the amount of stemwood produced per amount of absorbed light. In fertilized Eucalyptus plantations of Brazil, growth is expected to be strongly limited by light absorption in the first years after planting, when trees can benefit from high soil water stocks, recharged after clearcutting the previous stand. Other limiting factors, such as water or nutrient shortage are thought to increase in importance after canopy closure, and changes in allocation patterns are expected, affecting the LUE.

Studying changes in APAR and LUE along a complete rotation is paramount for gaining insight into the mechanisms that drive the inter- and intra-genotype variabilities of productivity and stemwood biomass at the time of harvest. Here, we present a 6-year survey of productivity, APAR and LUE of 16 Eucalyptus genotypes of several species used in commercial plantations and planted in 10 randomized replications in the São Paulo Region, Brazil. APAR was estimated using the MAESTRA tridimensional model parameterized at tree scale for each tree in each plot (a total of 16000 trees) using local measurements of leaf and canopy properties. Stand growth was estimated based on allometric relationships established through successive destructive biomass measurements at the study site.


Allometric relationships predicting biomass of tree components, leaf surface, crown dimension and leaf inclination angle distribution throughout the rotation for the 16 productive genotypes are shown. Results at stand scale showed that 1) LUE increased with stand age for all genotypes, from 0.15 at age 1 yr to $1.70 \mathrm{~g} \mathrm{MJ}^{-1}$ at age 6 yrs on average; 2) light absorption was a major limiting factor over the first year of growth ( $\mathrm{R}^{2}$ between APAR and stand biomass ranging from 0.5 to 0.95 ), explaining most of the inter- and intra-genotype growth variability; 3) at rotation scale, the variability of final stemwood biomass among genotypes was in general attributable to other factors than average APAR; 4) differences in stemwood productions among genotypes remained large throughout the rotation; 5) LUEs over the second half of the rotation, rather than initial growth or APAR, was the major driver of stemwood biomass at the time of harvest.

Keywords: eucalypt clone, light interception, productivity, tropical plantation, production ecology, leaf area index

## 1. Introduction

In recent years, trade of wood products has increased sharply in response to the growing demand for industrial wood (e.g, particle board), paper and cardboard, coal for industry (e.g, iron and steel), among other products. This increase in wood demand is expected to strengthen in the future $(+20 \%$ by 2060 , Elias and Boucher (2014)). Given the depletion of the natural forest resources, the area of productive forest plantations has sharply increased (Elias and Boucher, 2014). Planted forest areas increased from 168 to 278 million hectares between 1990 and 2015 (FAO, 2015; Keenan et al., 2015; MacDicken, 2015). Forest plantations are providing an increasing share of the world's wood products, representing $6.9 \%$ of total forest area in 2012 ( $1.8 \%$ in South America), but responsible for $46.3 \%$ of the roundwood production ( $89.8 \%$ in South America) (Payn et al., 2015). Under appropriate policies and market regulations, commercial forest plantations are one of the options to tackle the current global forest degradation and deforestation by substituting wood products from natural forests (Pirard et al., 2016).

Eucalyptus plantations account for $33 \%$ of tropical forest plantations, with ca. 20 Mha planted worldwide (Iglesias-Trabado et al., 2009). In 2016, Eucalyptus plantations covered 5.67 Mha in Brazil, mostly for industrial use and located in the southern half of the country (IBA, 2017). The average production of Eucalyptus plantations in Brazil is $35.7 \mathrm{~m}^{3} \mathrm{ha}^{-1}$ year $^{-1}$, managed in rotations of 6 to 8 years (IBA, 2017). With gross primary productivity (GPP) of about $4.2 \mathrm{~kg} \mathrm{C} \mathrm{m}^{-2} \mathrm{yr}^{-1}$ and net primary productivity (NPP) of up to $3 \mathrm{~kg} \mathrm{C} \mathrm{m}^{-2} \mathrm{yr}^{-1}$ (Stape et al., 2008; Ryan et al., 2010; Nouvellon et al., 2012; Epron et al., 2013), these planted forests rank among the most productive ecosystems in the world (Luyssaert et al., 2007).

Large disparities do exist, however, with observed productivities ranging from 20 to $60 \mathrm{~m}^{3} \mathrm{ha}^{-1} \mathrm{year}^{-1}$ among plantations, as a result of contrasting pedoclimatic conditions, genetic material and management (Gonçalves et al., 2013; Binkley et al., 2017). To reach the highest productivities, local genetic improvement through breeding programs have been conducted in the main Eucalyptus cultivation areas of Brazil, aiming to increase adaptation to different environmental contexts. Eucalyptus species or hybrids are planted in a rainfall range from 500 to 2000 mm and an average annual temperature range from 19 to $27^{\circ} \mathrm{C}$ (ABRAF, 2012).

Breeding programs are primarily focused on production performance and wood quality at the time of harvest, which integrates de facto genetic potential, and its interaction with management, pedoclimatic conditions and resistance to biotic and abiotic stresses. Building on the high diversity of resource acquisition and ecological strategies found among Eucalyptus species and provenances (Drake et al., 2015; Pfautsch et al., 2016; Aspinwall et al., 2019) the genetic materials currently in use display a broad range of physiological, structural, biochemical and life history traits (Gonçalves et al., 2013). However, the biological mechanisms and associated traits responsible for the differences in final trunk biomass production and wood quality remain unclear, mostly because of the high covariation commonly observed among traits (Reich, 2014). Process-based models calibrated using local measurements of functional traits and evaluated against carbon and water cycling data have proved useful to untangling the mechanisms responsible for forest productivity (Marsden et al., 2013; Christina et al., 2015; Guillemot et al., 2015). Furthermore, the variability of soil and climate conditions occurring at both local and regional scales affects the intra-genotype variability of productivity, which hinder the quantification and analyse of intergenotype variability. Performance comparisons among genotypes are therefore conducted in forestry trials that aim at controlling the variability attributable to soil and residue management (Gonçalves et al., 2007; du Toit et al., 2010), fertilization (Laclau et al., 2009), water supply (Stape et al., 2008), rainfall exclusion (Battie-Laclau et al., 2014), stocking (Stape and Binkley, 2010; Crous et al., 2013; Resende et al., 2018), genotypes (Pallett and Sale, 2004; Silva et al., 2016) or a combination of these effects (Binkley et al., 2017).

Large differences in leaf size, foliage area per tree, spatial distribution of leaf area within the canopy, leaf inclination angles, optical properties and crown dimensions are observed among genotypes, resulting in different light absorption capacities. Light absorption capacity is thought to be a major factor limiting growth at tree scale across a broad range of environmental contexts and management (Binkley et al., 2010; Binkley et al., 2013; Campoe et al., 2013). At stand scale, however, the positive effect of light absorption on GPP and biomass production (Russell et al., 1989; Wang et al., 1991; Will et al., 2001) can be obscured by other limiting factors (Landsberg and Waring, 1997). For instance, Marsden et al. (2010)
showed that the total absorbed radiation (APAR) was well related to productivity among stands planted with the same Eucalyptus genotype in the first two years after planting, but vanished afterward. One reason could be the influence of water deficit on tree growth which is much larger after canopy closure (Christina et al., 2017; Christina et al., 2018). The effect of light absorption on forest productivity is also expected to vary among genotypes, soil, climate and management conditions (Forrester et al., 2018). Heterogeneity within a stand was shown to partly explain differences in production for a given genotype, higher heterogeneity reducing significantly the productivity (Binkley et al., 2010; Ryan et al., 2010; Stape et al., 2010; Luu et al., 2013). Heterogeneity could also explain differences of production observed among genotypes, e.g. if some genotypes show more tendencies towards heterogeneity and competition than others (Resende et al., 2016; Soares et al., 2016; Resende et al., 2018).

The present study aims at exploring the age-related changes in APAR, and the relationship between light absorption and stemwood production across 16 contrasted Eucalyptus genotypes at stand scale. In other words, our main objective is to test whether differences in stem production among genotypes are mostly related to differences in APAR or to differences in the light use efficiency for stemwood production (LUE), or both. The following specific questions are addressed:

- What are the changes of tree growth and APAR along the rotation?
- Which traits explain the differences in APAR among genotypes (e.g. leaf area index, leaf optical properties, leaf inclination angles or canopy clumping)?
- How does LUE vary among genotypes, and how does it correlate with annual growth?
- Does within-stand heterogeneity of tree sizes explain the variability of production among clones?
- How do the drivers of stemwood production change across a local gradient of soil properties?

Sixteen genotypes from different origins were compared in a randomized block design set up at a single site in the field, in order to reduce the effects of changes in soil, climate and management on the intergenotype comparisons. The studied genotypes were selected among the most productive ones from the South to the North of Brazil. Each selected genotype has good performances in some pedo-climatic conditions of Brazil, but these conditions do not necessarily correspond to the local conditions of the field trial in our study. This was expected to lead to a large range of wood productivity, and thus useful to gain insight into the mechanisms underlying genotype performances.

## 2. Material and Methods

### 2.1. Study site and experimental design

The experiment was set up within a commercial plantation of 90 ha located in the State of Sao Paulo, south-eastern Brazil, at $22^{\circ} 58^{\prime} 04^{\prime} ' S$ and $48^{\circ} 43^{\prime} 40^{\prime}$ 'W, 750 m.a.s.l. and managed by the EUCFLUX project, from the Forestry Science and Research Institute (http://www.ipef.br/eucflux/en/). It consisted in 10 repetitions (blocks) of 16 plots (Figure 1a), each plot being planted with one different Eucalyptus genotype (G1 to G16, Table 1). Each block was made of a 4 x 4 grid of 16 plots where genotypes were randomly distributed (Figure 1b). Each plot was planted with a single genotype with a tree spacing of $3 \times 2$ $\mathrm{m}\left(1666\right.$ trees $\left.\mathrm{ha}^{-1}\right)$. Each plot was $36 x 32 \mathrm{~m}$ large and contained 12 lines of 16 planted trees. Only the 100 central trees are studied to avoid border effects between plots. An entire block had therefore a size of $144 \times 128$ meters. All blocks were managed following the standards currently used by Brazilian Eucalyptus plantation companies (Gonçalves et al., 2013) throughout the entire rotation. The experiment was planted in November 2009. The mean annual rainfall was $1430 \mathrm{~mm} \mathrm{y}^{-1}$ over the study period, $85 \%$ of this amount occurring between October and May, which is the period with high incoming global radiation (Christina et al., 2017). The 10 blocks were distributed over the 90 ha commercial plantation, which topography was mostly flat, excepted some slight declivity in the North-western and North-eastern parts of the area, down to a small river (see the riparian natural vegetation on Figure 1a). The soil was a deep Ferralsol over the whole area but the slight declivity was associated with a gradual change in soil texture properties (Campoe et al., 2012), from sandy soils upward (including blocks B1 to B7) to more clayish soils downward (blocks B8, B9 and B10). A complete physical and chemical description of the soil profile was performed in Pinheiro et al. (2016). A long-term ecosystem observatory at the center of the 90 ha stand, was equipped with a complete meteorological station and an Eddy-covariance tower (Nouvellon et al., 2010; Christina et al., 2017; Nouvellon et al., 2018). We surveyed the experiment for 6 years, which corresponds to the standard rotation duration of commercial Eucalyptus plantations for industrial roundwood in Brazil.

### 2.2. Stand inventories

All trees of the inner plots were individually surveyed for diameter at breast height $(\mathrm{DBH})$ and tree height (H). DBH measurements were made at 8 dates in all blocks (i.e. 100 trees x 16 plots x 10 blocks $=16,000$ trees), and at 5 additional dates in a subset of blocks (Table 2). H measurements were made on all trees during the first two years and on a subset of 24 central trees per plot afterwards (Table 2). Power relationships between measured DBH and H were established on these 24 trees to estimate H for the nonmeasured trees. DBH of all border trees were measured twice during the 6 years, and their values for
other dates were obtained using between-date relationships calibrated on the inside plot measurements of the same genotype and same block. H of border trees was then computed using $\mathrm{DBH}-\mathrm{H}$ power relationships calibrated on measurements in the inner plot at the same date. Finally, tree DBH and H in the plots (including border trees) were linearly interpolated at daily time step, for each tree and for the 6 years. The percentage of dead trees was recorded at each inventory date (hereafter called "mortality"). The GINI Index was also computed: this heterogeneity index can be used to evaluate the within plot competition between trees, using distributions of tree basal areas. It is based on the Lorenz curve and proved to be efficient at quantifying differences in stand structures among diverse forest management systems (Cordonnier and Kunstler, 2015; Fernández-Tschieder and Binkley, 2018). It was computed using the lorenz.curve function of the lawstat package of R software (v3.5.1). The higher the index, the more competition among trees.

### 2.3. Tree biomass measurements

Destructive sampling of trees for biomass, leaf area, crown dimensions, leaf angles, and leaf optical measurements were performed at 5 dates over the 6-year survey (Table 2) in all genotypes. At each date, 12 trees per genotype were sampled. Sampled trees were distributed among blocks (Table 2) and selected to encompass the DBH range measured in the inventories, which is the method generally adopted for these eucalypt plantations (Laclau et al., 2008). Only border trees were cut to avoid as much as possible perturbations and changes in tree growth in the inner plots.

After felling the tree, the height of the crown base and crown length was measured. The tree was then cut at crown base, the crown was straighten up vertically to measure leaf angle and crown radius (in the row and inter-row directions). Note that felling the tree did not damage the crown. Leaf angle distributions were measured on these 12 sampled trees per genotype. In each tree, 72 leaves were selected for angle measurement 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 between the basis 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 $10^{\circ}$ intervals for each genotype and each date.

Felled tree compartments were then weighted in the field, separating trunk (diameter $>2 \mathrm{~cm}$ at the thinnest end), living branches, dead branches and leaves. Subsamples of stemwood, bark and branches were taken to the laboratory and weighted before and after drying until constant weight. For leaf biomass, the green crown length of felled trees was divided into three equal-length sections (lower, middle and
upper). All leaves were weighted immediately after tree fall for each section. Twenty-five leaves were randomly selected for each crown section and kept cold until their fresh mass and area were measured in the laboratory. Trunk, bark, branch and leaf subsamples were then dried at $65^{\circ} \mathrm{C}$ until constant weight. Average dry matter content (ratio of the sample dry mass over the fresh mass) were calculated for each tree and combined to field-based fresh weight to calculate the dry biomass of all tree components. The leaf area of each crown section was calculated by multiplying the total field-based fresh mass by the leaf area to fresh mass ratio (calculated on the 25 sampled leaves). Single-tree leaf area and leaf biomass were computed by summing the values of each crown sections.

We measured the optical properties of leaves of each genotype at 1 and 6 years of age in two different blocks (Table 2) in 3 trees of different size, with 6 leaves measured per tree ( 3 crown sections * 2 samples), totalizing 1152 single leaf measurements. The reflectance and transmittance of these leaves were measured in the visible and near infrared spectra with an ASD FieldSpec Pro (Analytical Spectral Devices, Boulder, Colorado, USA) spectrometer and a Licor integrating sphere (Oliveira et al., 2017). SPAD measurements, which are highly correlated with leaf chlorophyll content per unit of leaf area, were performed on the same leaves with the Chlorophyll Meter SPAD-502 (Minolta Camera, Osaka, Japan), averaging 5 to 10 SPAD readings per leaf. A supplementary SPAD measurement was done at 4.6 years of age (Table 2).

### 2.4. Allometric relationships calibrations

After having tested many forms of age-related allometric equations issued from Saint-André et al (2005) and Picard et al. (2015) (not shown), we found that Equation (1) was the most precise and flexible to predict trunk and living branch biomass:
$Y=a * a g e^{b} * D 2 H^{c * a g e^{d}}$ Eq. 1

Where Y is the variable to predict (trunk or branch biomass). D2H is the product of squared $\mathrm{DBH}\left(\mathrm{m}^{2}\right)$ and $\mathrm{H}(\mathrm{m})$, age is the age of the trees (in years as in Table 2), $a, b, c$ and $d$ are parameters to be estimated. Parameters were fitted using the $n l s$ function of R software. For a given genotype, we tested two fit options: one with the data from all blocks, and another including a "site" effect, i.e. fitting two different equations, one for blocks B1 to B7 (sandy blocks) and another for B8 to B10 (clayey blocks, Fig. 1). Model selection was based on Akaike Information Criterion (AIC).

For leaf area and leaf biomass, a genotype-specific allometric relationship was calibrated at each inventory date (without age effect), with the following equation:
$Y=a * X^{b}$
Eq. 2
Where Y is the variable to predict (leaf area or leaf biomass), and X is either DBH or D2H. As before, a model selection procedure based on AIC was used to select the best predictor (DBH or D2H) and select between one common equation for all blocks or two different equations for sandy and clayey blocks.

After applying the final allometric equations to each tree measured at each inventory date, Leaf Area Index (LAI, $\mathrm{m}_{\text {leaf }}^{2} \mathrm{~m}^{-2}$ soil) was computed by summing the calculated tree leaf area of all trees within each plot and dividing the result by the plot areas. Specific Leaf Area (SLA, $\mathrm{m}^{2} \mathrm{~kg}^{-1}$ ) was obtained by dividing the total leaf area of the plot by the sum of the tree leaf biomass of all trees of that plot. Time interpolation of tree leaf area between the inventory dates was done following the methodology adopted in other studies, using remote-sensing data to account for the seasonal dynamics of tree leaf area and LAI (le Maire et al., 2011; le Maire et al., 2013; Christina et al., 2017).

Other allometric relationships were calibrated to estimate tree dimensions needed for MAESTRA model simulations: crown diameter (D) in the directions of the planting row and the inter-row (Equation 3) and the crown ratio (CR), which was the ratio between the crown height and the total height of the tree (Eq.4). Single equation per genotype for all blocks and using DBH had systematically lower AIC.
$D=a * a g e^{b} * D B H^{c * a g e} \quad$ Eq. 3
$C R=a * a g e^{b} *(D B H+c)$
Eq. 4
Finally, the dependency of Leaf Inclination Angle (LIA) to height was explored. Leaf angles are indeed commonly observed to vary along a vertical gradient in forests, from sun leaves on the top of the canopy having large angles to more horizontal leaves at the bottom of the canopy (Russell et al., 1989; Posada et al., 2009). From destructive measurements, average leaf angle per section of crowns (three sections: top, middle and bottom) was associated to the central height of this crown section. The following equation was fitted for each genotype:
$L I A=a * a g e^{b} * H_{m}{ }^{a g e^{c}} \quad, \quad$ Eq. 5
where $\mathrm{H}_{\mathrm{m}}$ was the measurement height, i.e. the height from the soil to the middle of the crown section where the angles of the leaves were measured. The standard deviation of LIA was constant across measurement height.

### 2.5. Simulations of fAPAR, Extinction Coefficient, and LUE

The MAESTRA processed-based model (Medlyn, 2004) is an improvement of the MAESTRO model (Wand and Jarvis 1990). The light interception calculation is based on Norman and Welles (1983) and is described in other studies (Wand and Jarvis 1990, Medlyn 98, Bauerle 2004). The MAESTRA model has been applied in many other studies dealing with Eucalyptus plantations (Campoe et al., 2013; le Maire et al., 2013; Christina et al., 2016; Christina et al., 2017; Christina et al., 2018; Vezy et al., 2018), and a detailed description of the model and parameterization for different Eucalyptus plantations can be found in these studies.

The model was parameterized for the 16 genotypes in all 10 blocks (Figure 1b). For each block, all trees were described in the model, including border trees in all the plots. Parameters at tree level were: position in the plot ( $\mathrm{x}, \mathrm{y}$ ), height, crown height, crown radius in the row and inter-row directions and leaf area, which were obtained by applying the allometric equations (Section 2.4) to tree inventories. Leaf inclination angle distribution was computed at plot scale, for each genotype, block and date, after having applied the Equation (5) to all crown sections of all trees of the inventories and weighted by their section leaf areas. Other parameters such as reflectance and transmittance of leaves were averaged at genotype level, and linearly interpolated between measurements dates. The same horizontal distribution of leaf area density within crowns were used for all genotypes, because no local measurements were available (values from Christina et al. (2016) in a neighbouring stand). Meteorological data used in these simulations consisted in half-hourly gap-filled (only $0.15 \%$ of missing data) global radiation converted to Photosynthetically Active Radiation (PAR), that was measured on top of the eddy-covariance tower (Figure 1a) during the entire simulation period.

Simulations were performed at half-hourly time-step, in all inside plots of all blocs (i.e. for 16,000 trees). To speed-up the computation time, we chose to perform simulations of one day every 20 days. The ratio of the sum of the radiation absorbed by all within-plot trees (APAR) to incident PAR is the fraction of absorbed PAR (fAPAR). Daily fAPAR was computed for these simulated days and interpolated in time for each plot. Daily APAR of non-simulated days were estimated as the product of interpolated fAPAR and the incident PAR. Annual values of fAPAR were also computed as the annual sum of APAR divided by annual sum of incident PAR.

As PAR absorption is influenced by many canopy structural parameters other than LAI (crown size and shape, LIA, Leaf optical properties, etc), we computed effective extinction coefficients for daily PAR absorption in order to assess the overall effect of these parameters. Extinction coefficients (k) were
computed for each plot with a non-linear regression of the following simplified and widely used equation (Landsberg and Hingston, 1996; Almeida et al., 2004), for each year:
$f A P A R=1-\exp (-k * L A I)$,
Eq. 6
where fAPAR is the fAPAR computed over the annual period and LAI is the averaged LAI at the same dates.

APAR was further used to compute the light use efficiency for NPP of stemwood (LUE, $\mathrm{g} \mathrm{MJ}^{-1}$ ):
$L U E=\frac{N P P_{\text {stem }}}{A P A R}, \quad$ Eq. 7
where $N P P_{\text {stem }}\left(\mathrm{g} \mathrm{m}^{-2} \mathrm{y}^{-1}\right)$ is the annual Net Primary Production of stemwood biomass at plot level. $N P P_{\text {stem }}$ is different from the stemwood biomass variation $(\Delta B) . \Delta B$ is computed as final minus initial living stem biomass during a time period, and is further used in the manuscript as "stemwood biomass growth". $N P P_{\text {stem }}$ is the sum of $\Delta B$ and the biomass of trees that died during the same time period. APAR is the total PAR absorbed by the plot during the same period. Growth Efficiency (GE, $\mathrm{g} \mathrm{m}_{\text {leaf }} \mathrm{y}^{-2}$ ), also called Leaf Area Efficiency, was similarly computed as the ratio of $N P P_{\text {stem }}$ and LAI.

### 2.6. Model validation

Simulated APAR is difficult to validate against measurements, since APAR cannot be measured easily on a large number of plots. Instead, as in other studies (Charbonnier et al., 2013; le Maire et al., 2013; Christina et al., 2015), we validated another simulated intermediate variable, which is of high importance in the APAR simulation: the gap fractions (GF) as a function of view angles. We compared the measured and simulated directional GF at ground level, as in Roupsard et al. (2008). Canopy structures strongly varied among genotypes, as illustrated with vertical upward pictures in Figure 2, which allowed testing the MAESTRA model on a large range of light interception conditions.

Measurements of directional gap fractions (GF) were conducted using two LiCor PCA LAI-2000 (Li-Cor, Lincoln, NE, USA) on June 2014, in all plots of blocks B2, B3 and B8 (Table 2). In each plot, 12 measurements were made below the canopy with one LAI-2000 device using a $180^{\circ}$ azimuthal field of view, with the viewing direction parallel to planting lines, in periods with ca. $100 \%$ diffuse incoming light. The locations of the measurements were distributed in a systematic grid to cover a large part of the plot and to sample points at different distances from the trees but never in front of a tree trunk (see positions in Figure 1b). Continuous measurements of incident radiation were performed simultaneously at the top of the central tower with the second LAI-2000, which was inter-calibrated with the first one and
which used the same measurement configuration (orientation and view cap). The ratio between belowand above-canopy measurements were computed for the five zenithal rings of the LAI-2000 fish eye lens and were used as an estimate of the directional gap fraction. Simulated GF at the same locations, angles and date were obtained from MAESTRA simulations. The simulated and measured angular GF values were then averaged per genotype and compared. The Diffuse Non-Interceptance (DIFN) values, computed as in the LAI-2000 manual (LI-Cor, 1992), were compared between simulations and measurements. The value of (1-DIFN) is a good proxy of the APAR of the canopy under diffuse conditions, even though leaf reflectance and transmittance and soil reflectance may affect the correspondence between both variables.

### 2.7. Statistical analysis

Half-hourly tree-scale simulations of MAESTRA were averaged over each plot (i.e. 10 plots for each of the 16 clones), and each year. As described before, the simulations were averaged annually, for each growing year. Statistical analyses were performed on variables that were all averaged over the same time periods. The analysis of observations and MAESTRA simulations were conducted using Pearson correlations and linear mixed models (lmer function of lme 4 package of R ). A linear mixed model between fAPAR and variables described in Table 3 was computed at each age, including blocks as random effect. We first performed a model selection based on the Variance Inflation Factors (VIF) in order to deal with multicollinearity among variables. Variables having highest VIF were iteratively removed one by one until all remaining variables had a VIF lower than 5. Then, we performed a simple backward elimination of non-significant effects of the linear mixed effects model, starting with the remaining variables after VIF elimination (step function of lmerTest). Final model F-test of fixed effects are computed using the Satterthwaite's method. Another more simple linear mixed models was computed between annual stemwood growth and genotype, APAR, GINI and blocks, with blocks as random effects. Fraction of variation attributable to each variable in regression model were computed using the calcVarPart function of the variancePartition package. Least Significant Difference (LSD) used in graphical representation of inter-genotype difference was computed using the LSD.test function of package agricolae.

## 3. Results

3.1. Time course of the characteristics of each genotype in each plot

## Allometric relationships

Allometric relationships predicting the biomass of tree components throughout the rotation for highly productive genotypes used in commercial plantations are illustrated in Figure 3 for genotype 14, and figures and equations for all other genotypes are given in Supplementary Material 1 "allometric relationships". Most of the relationships had high r-square and low Root Mean Square Error, allowing a precise estimation of single tree characteristics for all ages, genotypes and blocks. For some genotype, using distinct allometric equations for sandy (B1-B7) and clayey (B8-B10) areas yielded better fit of trunk and branch biomass. For tree leaf area (and therefore LAI and SLA), the allometric relationships changed between the sampling dates.

## Leaf area index

The average annual LAI increased during the first 2 years, to reach a peak value during the second year, and then decreased until the end of the rotation (Figure 4). The temporal evolution along the rotation was mostly similar among genotypes. Large differences in LAI were observed the second year after planting between genotypes, up to $3 \mathrm{~m}^{2} \mathrm{~m}^{-2}$. The genotype G16 showed the lowest LAI throughout the rotation, averaging $3 \mathrm{~m}^{2} \mathrm{~m}^{-2}$ (reaching a peak value of $4.2 \mathrm{~m}^{2} \mathrm{~m}^{-2}$ at 2.6 years old, data not shown), while the genotype G11 had the highest average LAI of $4.5 \mathrm{~m}^{2} \mathrm{~m}^{-2}$ (and a peak value of $6.5 \mathrm{~m}^{2} \mathrm{~m}^{-2}$ at 2.6 years old, data not shown). The LAI of the other genotypes were quite homogeneously distributed between these extremes, and differences between genotypes were significant each year. A seasonal decrease in LAI during the cold and dry season was observed in the data (data not shown). SLA decreased with age for almost all genotypes as observed in other works (Sands and Landsberg, 2002; Almeida et al., 2004; le Maire et al., 2011), and particularly for the seed origin G1 and G2 (Supplementary Material 4).

## Trunk biomass and tree growth

The time course of biomass of the stem, branch and leaves is presented in Figure 4. Stem biomass almost linearly increased during the 6 years of the rotation (Figure 4). The pattern was totally different for the biomass of living branches and leaves, which reached a plateau (branch biomass) or slightly decrease (leaf biomass) from the $3^{\text {rd }}$ year to the $6^{\text {th }}$ year after planting. Branches and leaves therefore accounted for a decreasing percentage of the total aerial living biomass, from $20 \%$ at the end of the third year to 5\% at the end of the rotation.

The differences in stem biomass among genotypes at the end of the 6-year survey were very large and highly significant. For instance, the biomass of G10 ( $21.5 \mathrm{~kg} \mathrm{~m}^{-2}$ ) was on average across the 10 blocks $35 \%$ higher than that of G15 ( $15.9 \mathrm{~kg} \mathrm{~m}^{-2}$ ) at age 6 years (Figure 5). Between these extremes, the 16 genotypes were fairly well distributed, some being significantly different from the others whatever stand age (Figure 4 and Figure 6). However, their ranking changed along the rotation, with some genotypes
such as G8 or G16 starting with a very strong growth until the fourth year, but then slowing down, while other genotypes (e.g., G5 and G10) steadily accumulated stem biomass throughout the rotation (Figure 4). Some genotypes, such as G9, exhibited a large difference in plot biomass and productivity among blocks, which tended to increase toward the end of the rotation due to outliers with low values (Figure 4). This was mostly due to an increase in tree mortality in some of their plots (Figure 4 and 6).

## Mortality and intra-plot competition

Mortality was generally low in the experiment, most genotypes having less than $5 \%$ of dead trees compared to stocking at planting, on average, at the end of the rotation (Figure 4 and 6). However, mortality was significantly different among genotypes, some genotypes (e.g., G1, G2, G3 and G13) being more severely affected than others. G1 and G2 were from seed origins and had higher number of dead trees since the first year of the rotation, while genotypes G3 and G13 displayed high mortality rates, possibly caused by a sensitivity to extreme wind. Some particular events occurred at some plots, such as a lightning strike, pathogen attack and other causes of tree dieback. Some blocks, such as B2, but more clearly B10, showed high mortality rate for all genotypes.

Competition among trees within plots is both the result of differences in tree development and spatial heterogeneity created by mortality of some trees. GINI heterogeneity index showed that the level of competition was in general low (GINI < 0.25) (Cordonnier and Kunstler, 2015; Fernández-Tschieder and Binkley, 2018). Competition intensity, as captured by Gini index, differed among genotypes: all genotypes followed a comparable trajectory with time, but at different absolute levels. The four genotypes showing the highest competition level also showed the highest mortality rates, and the highest heterogeneity in tree height (Figure 4). As expected, the two seed-origin genotypes (G1 and G2) had the highest GINI index. The GINI index decreased from the first to the second year, and then increased steadily with time for all genotypes. Standard deviation of tree height also increased along the rotation, meaning that tall tree grew faster in height than smaller ones.

## Leaf angles distributions and optical properties

Leaf inclination angle distributions were highly variables among genotypes and changed with time along the rotation. Illustration for two contrasted genotypes, G6 and G16 are given in Figure 7, and figures and equations for all other genotypes are given in Supplementary Material 2 "Leaf inclination angle distributions". Some genotypes had erectophile-like leaf angle distribution, such as the G14 or G16, while others tended to be more planophile (e.g. G3, G6). Changes of LIA with time was significant for some genotypes, progressively changing from a planophile-like distribution at young ages to more erectophile leaves (e.g. G1, G2, G3, G6, G8, G15). Other genotypes, on the contrary, did not show large
changes of LAD with time (e.g. G4, G9, G10, G16). All genotypes showed a clear leaf inclination change from the top to the bottom of the canopy, with more erectophile leaves at the top and more planophile leaves at the bottom (see Figure 7 and Supplementary Material 2). It is interesting to note that this trend is found in all trees, whatever their size within the canopy: top leaves of a small tree have similar angles than bottom leaves of tall trees.

The reflectance and transmittance of leaves were not statistically different between genotypes due to high within-genotype variability of leaves within the crown. The observed increase of SPAD values between age 1 and 6, for almost all genotypes (Figure 8 and Supplementary Material 4), is coherent with the decrease of reflectance and transmittance, which was accounted for in the light transfer simulations. SPAD values increased for almost all genotypes, and inter-genotype differences were high.

### 3.2. Validation of the light transfer modelling

Measured and modelled directional gap fractions were in close agreement for much of the genotypes (Supplementary Material 3 "MAESTRA validation", Figure SM3.1). There were substantial differences in gap fraction among genotypes, as visually observed in the field on the day of the measurements (Figure 2), which was well captured by the model. The vertical GF was more difficult to simulate accurately, because this angle integrated small canopy areas and was therefore more subject to uncertainties in tree positions and sizes, but the agreement between simulations and measurements is correct. The shape of the decrease of GF with view angle is related to the leaf angle distributions and dimensions and locations of the crowns and was also well simulated for most of the genotypes.

When comparing the simulated and measured (1-DIFN) variables, the correlation was high (Pearson correlation $\mathrm{r}=0.84, \mathrm{p}<0.001$ ) and the results were good for the three blocks were the measurements were carried on (Supplementary Material 3, Figure SM3.2). The results were slightly underestimated for high values and overestimated for low values. Large differences in (1-DIFN) among genotypes were well captured, which confirmed that the MAESTRA model was able to simulate APAR in contrasting stand structures.

### 3.3. Genotype differences in APAR and fAPAR

fAPAR increased rapidly during the first two years, and then reached a plateau with values between 0.8 and 0.97 (Figure 4). From the second year on, APAR interannual variation was therefore mostly driven by
changes in average annual incident PAR. The increase in fAPAR at the beginning of the rotation mostly resulted from the increase in LAI and crown diameter and height. A saturation of fAPAR when LAI reached approximately $3 \mathrm{~m}^{2} \mathrm{~m}^{-2}$ was observed for all genotypes along the rotation (Figure 4). Variations of fAPAR also resulted from other structural characteristics of the canopies taken into account in the MAESTRA modelling, such as crown size and shape, leaf inclination angle distribution, leaf distribution within crowns, and leaf optical properties. All these variations were summarized in the Extinction Coefficient variable (Figure 8 and Supplementary Material 4). Extinction coefficient showed an initial decrease until 3 years of age, followed by an increase, and large differences between genotypes. A simple mixed model predicting stem growth in function of the genotype and APAR and their interactions, with blocks considered as random effects, showed that APAR and genotype were always significant predictors, but that their interactions occurred only in the first four years (data not shown). So in the first years, the Growth vs. APAR relationship changed among genotypes, but the genotype principal effect on stem growth subsequently become stronger and independent of APAR.

A linear mixed model of fAPAR in function of plot averages characteristics, with all genotypes included and with the blocks considered as random effect, confirmed the highly significant importance of LAI all along the rotation (Table 3). LIA was also significantly affecting fAPAR all along the rotation, except for the $5^{\text {th }}$ and $6^{\text {th }}$ year. Plot average height significantly affected fAPAR along the rotation. Mortality had a significant effect in the $4^{\text {th }}$ year only, when several genotypes suffered from high mortality increase (Figure 6), which created gaps only partly compensated by increasing growth of neighbour trees. Finally, average optical properties were significant at explaining the inter-plot variations of fAPAR at the end of the rotation.

### 3.4. Genotype differences in Growth Efficiency and LUE

Growth efficiency (GE), a measure of the amount of stemwood produced per year and per unit of leaf area, was in general increasing along the rotation (Figure 4). The GE variability among genotypes was very high and significant, with some genotypes such as G16 having a very high GE at the beginning of the rotation that stabilized with stand age, while other genotypes had lower GE at the beginning but it increased steadily to reach high values at the end of the rotation (e.g., G10).

Similarly to GE, light use efficiency for stemwood production (LUE) increased during the rotation. However, some differences appeared between GE and LUE: the genotypes having high GE did not necessarily showed high LUE. These differences resulted from the non-proportionality between LAI and fAPAR (see section 3.3). The slight decrease observed in LUE in the $5^{\text {th }}$ year was mostly due to the slight increase in APAR during that year, which did not impact tree growth. This increase of APAR was mostly
attributable to an increase in annual incoming PAR. Despite being affected by inter-annual changes in growth conditions, the LUE showed a slightly increasing trend, consistent along the rotation. fAPAR was indeed almost constant for most of the rotation, while trunk growth slightly increased. Rotation averaged LUE, shown in Figure 9 c, show high difference among genotypes, with $29 \%$ higher value for G10 (1.35 $\left.\mathrm{g} \mathrm{MJ}^{-1}\right)$ than for G2 (1.05 $\left.\mathrm{g} \mathrm{MJ}^{-1}\right)$.
3.5. Drivers of the spatial variability of trunk growth in function of stand age and genotypes

Variability in LAI and APAR among genotypes did not explain variability in production (Figure 9 a, b) summed over the entire rotation. By contrast, the inter-genotype variability of LUE explained a large part of the variability in productivity (Figure 9c). In other words, genotypes with higher LAI, or absorbing more radiation along the rotation, did not systematically produce more stemwood. Other processes than light absorption, captured in the Light Use Efficiency for stemwood production, were responsible for differences in productivity among genotypes. However, LAI and APAR explained the spatial differences (inter-block) in stemwood production of some genotypes (e.g., G7 and G13, Figure 9 d, e). On an annual basis, the correlation was especially high and significant in the first year of the rotation, when the net primary production of stemwood was highly linearly related with APAR (Figure 10). In the first year, APAR explained most of the spatial variation of stemwood production. This production was however very low compared to subsequent years. From the second year on, some genotypes were more responsive to change in their APAR (e.g., G10 and G14) than others. The absence of a significant APAR-growth relationship was likely due to the absence of inter-block variability of APAR (e.g., G5), or of stemwood growth (e.g., G9). LUE explained most of the spatial variability of stemwood production (Figure 9 f). This was expected in this context since LUE was computed as the part of the productivity that was not directly explained by absorbed PAR. To summarize, the variability of wood production was primarily attributable to differences among genotype that were not captured by differences in APAR all along the rotation (Figure 11). APAR significantly explained growth differences among genotypes in the first year, in the fourth and at the end of the rotation, while GINI competition index (within-plot competition intensity) was observed to have a substantial effect at the middle of the rotation (from $2^{\text {nd }}$ to $4^{\text {th }}$ years). The block effect was significant all along the survey, but higher at the end of the rotation. Residuals, i.e. the part of the variance in stand growth not explained by these four variables, increased after 3 years of age.

## 4. Discussion

The Eucalyptus genotypes compared in our field trial were obtained from breeding programs located throughout Brazil, and large difference in production dynamics was expected among them when planted at a single location. The same planting date, stocking density and management practices over the study area make it possible to assess the consequences of genotype choice and spatial variability of soil resources on the dynamics of biomass accumulation in our field trial. The 10 blocks of the experiment were indeed located close to each other, thus experiencing a similar climate while soil characteristics substantially varied among blocks (Campoe et al., 2012). The large range of productivity observed among genotypes resulted in a valuable dataset for testing hypotheses on the effects of stand characteristics, allometry and functional traits on productivity for several species and hybrids within the Eucalyptus genus.

We observed that tree productivity was mainly driven by differences in genotypic performances. Indeed, after excluding the plot of B4-G9 having very high mortality rate (Figure 6), the correlation between the stem biomass of the most productive plots and the less productive plots among genotypes was high and very significant ( $\mathrm{r}=0.90$ and $\mathrm{p}<0.001$ ), which indicate that the most productive genotypes were consistently more productive everywhere in the whole area despite the soil gradient. Most of the clonal materials studied here had higher productivity than the two seed origin materials G1 and G2. To analyse the productivity of each genotype, we followed the framework of the production ecology equation that separates production into the product of resource supply, proportion of captured resource and efficiency of resource use (Monteith and Moss, 1977). Light supply was considered equivalent for all plots of the experiment, reducing the explained variation of productivity to variations of fAPAR and LUE for stem wood production. LUE for stem wood production captures a variety of processes such as photosynthesis per unit of absorbed light, which is function of the leaf photosynthetic characteristics and of the environment, living biomass respiration, and partitioning of assimilated carbon to stemwood production (Russell et al., 1989).

## Variations of APAR, fAPAR and extinction coefficient with genotype and stand age

Comparison between MAESTRA simulation and light interception measurements conducted in situ showed strong adequacy (Supplementary Material 3). The model successfully predicted angular gap fractions for all genotypes, i.e., it reproduced the absolute GF value in zenithal direction (mostly linked to LAI) as well as the GF diminution with angle view (mostly linked to leaf angle and directional clumping).
fAPAR and APAR increased in the first two years after planting for all genotypes, before stabilizing at fAPAR plateau values ranging from about 0.8 to 0.97 depending on the genotype. Similar dynamics of fAPAR were observed in other studies, based on model simulations (le Maire et al., 2013), or situ measurements and remote sensing data (Marsden et al., 2010). At all ages, genotypic differences in fAPAR were driven by LAI (Table 3). For all genotypes, LAI increased rapidly after planting, reaching a peak in the second or third year, and decreased afterward until the end of the rotation (Figure 4). This typical age-related pattern in LAI has been reported for many Eucalyptus plantations across the world (Ryan et al., 2004; Whitehead and Beadle, 2004; du Toit, 2008; le Maire et al., 2011). The decrease in LAI toward the end of the rotation did not strongly affect fAPAR, since LAI values remained at high levels for which the fAPAR vs. LAI relationships saturates. The genotypic variability in fAPAR was also explained by LIA and crown sizes (Table 3). Crown size has an impact on the macro-clumping of LAI, which was shown to enhance radiation transmission throughout the canopy and increase GPP (Rambal et al., 2003). Although potentially contributing to inter-genotype differences in APAR, micro-clumping inside tree crowns were not characterized in this study due to lack of data on the within-crown distribution of leaves.

The integrated effect of changes in canopy structure on APAR was however captured in the extinction coefficient $k$ for daily PAR absorption (Equation 6, Figure 8 and Supplementary Material 4). Daily extinction coefficients are useful for a simplified modelling of daily absorbed light from LAI and daily incident PAR. The values of $k$ estimated in the present study were in the 0.4 to 0.76 range. These values are on the higher range of measured values reported in literature (Albaugh et al., 2016). In the present case, $k$ estimated with MAESTRA considered the canopy properties, the course of the sun during the day and the separation of direct and diffuse radiation. Extinction coefficient for diffuse sky radiation are higher than for direct radiation, since extinction coefficients are lower at nadir when eventual direct PAR is higher (Nouvellon et al., 2000). On the contrary, diffuse extinction coefficient takes into account the whole hemisphere, where nadir solid angles are under-represented compared to higher angles which have higher directional $k$ values. It underlines the necessity to distinguish the direct and diffuse radiation when computing APAR (Li and Fang, 2015), as done in MAESTRA.

A decrease of the extinction coefficient between two and three years of age was also observed by Dovey and Du Toit (2006), with lower values (from 0.55 to 0.42 ). Lower $k$ values were obtained at LAI peak, probably due to the decrease of diffuse extinction coefficient with LAI increase (Nouvellon et al., 2000). Differences between genotypes stayed along the rotation. Our results therefore showed that genotype- and age-specific values of extinction coefficient are needed when using Equation (6) for computing fAPAR,
while most of modelling studies are using a default value of 0.5 (Landsberg and Hingston, 1996; Almeida et al., 2004; Pérez-Cruzado et al., 2011).

Despite a rather simple representation of the 3D structure of canopies, other studies show that MAESTRA is flexible enough to represent various types tree crowns, and fast enough to simulate APAR over entire rotations (Bauerle et al., 2004; Binkley et al., 2010; Charbonnier et al., 2013; Gspaltl et al., 2013; le Maire et al., 2013). On the present study, MAESTRA accounted for variation of LIA at plot scale, explaining large part of the APAR variation (Table 3). It confirmed that this variable should be systematically estimated together with LAI when analysing Eucalyptus plantations APAR. Detailed representation of specific tree traits such as vertical profiles of within-crown leaf inclination angles or leaf area distribution would request more complex measurements and models, such as 3D structural models describing each leaf orientation (Parveaud et al., 2007). Gradient of inclination angles from erectophile on the top to planophile on the bottom of the canopy is known as optimal for maximizing canopy photosynthesis and limiting leaf photoxidative, temperature or water stresses associated with high irradiance (Russell et al., 1989; King, 1997; Posada et al., 2009). Such optimality seems to be genotypedependent, and further studies are needed to examine the effect of LAI and leaf angles, together with other variables such as SLA, nitrogen and photosynthetic parameters profiles on productivity. Leaf optical properties were shown to have significant effect on fAPAR differences among genotypes. Correlation of SPAD with PAR reflectance and transmittance observed in our dataset could facilitate the field estimation of these characteristics. Finally, row orientation was accounted for in the MAESTRA simulation but its effect on daily APAR and GPP was not studied here. A model such as DART (Gastellu-Etchegorry et al., 2004), can help understanding further differences in light absorption regimes among genotypes and locations, as was done in the same experiment in Oliveira et al. (2017).

## Variations of LUE with genotype and stand age

The values of Light Use Efficiency for stemwood production obtained in the present study were in line with measurements from previous studies led in Eucalyptus plantation in Brazil (Marsden et al., 2010; le Maire et al., 2013), which showed similar patterns of strong increase at early age and saturation or moderate increase after canopy closing. Light Use Efficiency is driven by a complex set of processes ranging from leaf-scale to tree-scale levels (Binkley et al., 2010) that need to be untangled to understand the age-related trend observed in our trial. LUE and GE have different trends along the rotation, GE showing less saturation due to increase of the APAR/LAI ratio after canopy closure. The photosynthetic capacities of the leaves may change among genotypes and site conditions, but they were not measured in
this study. SPAD values averaged at stand scale, related to chlorophyll content (Pinkard et al., 2006), increased with tree age (Figure 8), but the link with photosynthetic capacity, and consequently LUE and GE, is not straightforward and would require more investigations.

Gross photosynthesis can also be strongly impacted by drought periods, through changes in stomatal conductance and eventually through leaf fall. There are large differences of leaf anatomy between these genotypes, and sap flow measurements have also shown large differences in tree transpiration per unit of leaf area in our experiment (unpublished data). Previous studies led in the same stand (Christina et al., 2017) or in a close rainfall exclusion trial (Christina et al., 2018) have shown that in this region, Eucalyptus plantations established in deep sandy soils have access to important soil water stocks in the first years after planting. Water stress therefore starts affecting plantation functioning and productivity only after canopy closure at about 2 years of age. Our results suggest that this could also be the case for most of the genotypes in the studied trial, but no measurements were made to confirm this hypothesis.

Partitioning of the photosynthesized carbon between respiration and allocation to tree organ is probably a major driver of the changes in LUE with age, among genotypes and among sites. Indeed, partitioning is predominantly oriented toward resource-capturing organs at the beginning of the rotation (especially the first year) and toward woody organs latter in the rotation (Nouvellon et al., 2012; Marsden et al., 2013). Shifts in carbon allocation with ontogeny, environmental constraints and resource availability was also observed in Ryan et al. (2004) in another Eucalyptus genotype. Carbon partitioning to aboveground NPP is also spatially variable: higher GPP and carbon partitioning to stemwood generally occurs in more fertile sites (Haynes and Gower, 1995; Stape et al., 2008; Campoe et al., 2012; Vicca et al., 2012). Increasing soil nutrient availability can also enhance the carbon partition to aboveground tree components (Giardina et al., 2003; Litton et al., 2007; Epron et al., 2012). Water availability and stand structure also alter carbon partitioning, e.g. between aboveground and belowground (Ryan et al., 2004; Stape et al., 2008).

## Effects of stand heterogeneity, tree mortality and soil properties on growth and LUE

In general, mortality is low in commercial Eucalyptus plantation managed in short rotations, but it was relatively high for some blocks and genotypes in our study as a result of tree fall after windy events, lightning strikes, etc. Contrasting sensibilities of the 16 genotypes to wind and pathogens led to significant differences in mortality rates. Mortality created or reinforced heterogeneity in tree size within canopies by creating gaps. In this study, seed-origin plantations (G1 and G2) and clones G3 and G13 showed higher mortality rates. Heterogeneous canopies of Eucalyptus were shown to have lower
productivity (Binkley et al., 2010; Ryan et al., 2010; Stape et al., 2010; Luu et al., 2013). Similar conclusions were found in monospecific European forests (Bourdier et al., 2016). Here, the effect of stand heterogeneity was assessed with two indices, the GINI index of tree basal areas and standard deviation of height of living trees. Heterogeneity is especially high for seed-origins genotypes G1 and G2, which probably reflects the heterogeneity of growth potential between seeds. Beyond biotic and abiotic mortality events, the heterogeneity of clonal plantation is also the consequence of differences in the planting conditions of each single tree. We observed that the GINI index of heterogeneity had a high and significant effect on clone productivity (Figure 11).

## Contrasted light-use strategies among genotypes of the Eucalyptus genus

A large diversity of trait combinations can be pointed out among the 16 highly productive genotypes in our experiment. For example, some genotypes with contrasting profiles:

- G10 with high LAI and branch biomass, high LUE and GE, low mortality and heterogeneity indices, strong growth at the end of the rotation in $5^{\text {th }}$ and $6^{\text {th }}$ years due to increase in LUE;
- G16 with low LAI and branch biomass, high leaf inclination angles, strong initial growth, low heterogeneity indices, high LUE and GE at the beginning of the rotation but a clear slowing down of LUE after 4 years, which result in a stem growth decline at the end of the rotation;
- G12 with low LAI and branch biomass, but high LUE and GE at the beginning but also at the end of the rotation, which displayed high biomass at 6 years
- G2 with high intra-stand heterogeneity of growth, high mortality, high branch biomass but average LAI, and lower LUE than average, which resulted in low standing biomass at 6 years

Such trait combinations show contrasting strategies for resource acquisition and growth. Our results highlight the major importance of the two last years of the rotation to maximize the amount of stemwood harvested at age 6 years. Indeed, the ranking of the genotypes changed substantially between the $4^{\text {th }}$ and $5^{\text {th }}$ year after planting (Figure 5). It underlines differences in resource acquisition dynamics and allocation among genotypes of the Eucalyptus genus. This was confirmed by a mixed model which showed that the final average stem biomass for each genotype was more closely explained by the average LUE of the $4^{\text {th }}$, $5^{\text {th }}$ and $6^{\text {th }}$ years ( $\mathrm{R}^{2}$ of $0.45,0.64$ and 0.61 respectively, all significant at $\mathrm{p}<0.01$ ) than by the LUE of the previous years (correlation unsignificant). The genotypes with the highest final biomass, such as G10 and G12, were the ones with the highest final LUE.

An hypothesis to explain these differences is that after 3 years old, several factors start affecting stemwood growth with different intensity among genotypes: water resource becomes a strong limiting factor since all the annual rainfall (about 1500 mm ) is used by the trees (Christina et al., 2017), hydraulic limitations may happen due to tree height (Ryan et al., 2006), and tree height could enhance susceptibility to wind damage. Other characteristics such as initial growth rates, stand homogeneity and APAR, were not as important as LUE during the last years to explain stemwood biomass at harvest for our 16 genotypes. However, the diversity of growth patterns at the end of the rotation in our study is probably influenced by the heterogeneity of the genotypes selected by forest companies from the South to the North of Brazil. It underlines the fact that clonal selection is more reliable at harvesting age, which is mostly the case in Brazil, but a more juvenile selection (around age 3 years) may still be valuable in forest companies to rank less diverse genotypes adapted to specific climate and soil conditions.

An interesting trend, not analysed in details in the present study, is that genotypes having invested more in leaves were generally more adapted to wet regions, such as G14 (E. saligna coming from a region having mean daily temperature of $18.4^{\circ} \mathrm{C}$, with $13.2-24.2^{\circ} \mathrm{C}$ range, and rainfall of $\sim 1600 \mathrm{~mm}$, Table 1), while genotypes having lower LAI were more conservative for water use, such as G16 (E.grandis $x$ E. camaldulensis selected in a region having mean temperature of $24.7^{\circ} \mathrm{C}$, with $22.4-26.1^{\circ} \mathrm{C}$ range and rainfall of $\sim 1000 \mathrm{~mm}$ ). They also have contrasting investments in fine roots, which could results in different abilities to access during dry periods to large amounts of water stored in the deep soil layers. In our experiment, Pinheiro et al. (2016) have shown at age 2 years that the fine root biomass was different between genotypes. The genotype with the highest fine root biomass, fine root length, and the maximum depth reached by fine roots was the genotype with the lowest leaf area index. However, this investment in fine roots at two years of age do not seem related to the final stemwood production at age 6 years, but the four genotypes studied in Pinheiro et al. (2016) were among the genotypes with the lowest biomass at harvest in our study (G1, G8, G14, G16). Modelling the differences of carbon cycling between genotypes using process-based models would be useful to gain insight into the processes driving the changes in LUE over the last years of the rotation.

## 5. Conclusion

As expected, the range of productivities was large in our study for Eucalyptus genotypes originating from breeding programs located across a large climate gradient and grown in a single location. Productivity
was analysed here together with other characteristics of the stands, such as their leaf area index, level of stand heterogeneity, and other functional traits. The genotypes showed large differences in dynamics of LAI, APAR and in efficiency for using the absorbed APAR to grow wood. Differences of LAI and APAR among genotypes were not linked to genotype productivity. Spatial variability of growth was directly related to APAR for almost all genotypes the first two years after planting. Over the entire rotation, only 5 out of 16 genotypes showed significant correlation between total absorbed PAR and stemwood production. The efficiency for converting radiation into stemwood is the major factor explaining i) differences of productivity among genotypes, and ii) explaining differences of productivity of a given genotype along a gradient of soil characteristic. LAI and LUE dynamics along the rotation were clonedependent. The LUE at the end of the rotation was the major factor differentiating the highly productive from the less productive genotypes at age 6 years in monoclonal Eucalyptus plantations. The biological mechanisms, and associated functional traits, that drive spatial and temporal changes of LUE in commercial Eucalyptus plantations deserve closer attention.

## 6. Acknowledgements

This project was funded by the EUCFLUX project (cooperative program with Arcelor Mittal, Cenibra, Bahia Specialty Cellulose, Duratex, Fibria, International Paper, Klabin, Suzano, and Vallourec Florestal), coordinated by the Forestry Science and eserach Institute - IPEF (https://www.ipef.br/). The experiment also partially benefited of fundings from Agence Nationale de la Recherche (MACACC project ANR-13-AGRO-0005, Viabilité et Adaptation des Ecosystèmes Productifs, Territoires et Ressources face aux Changements Globaux AGROBIOSPHERE 2013 program) and the FAPESP-Microsoft Research project SEMP (Process n. 2014/50715-9). The experimental site is part of the SOERE F-ORE-T, which is supported annually by Ecofor, Allenvi and the French National Research Infrastructure ANAEE-F (http://www.anaee-france.fr/fr/). We acknowledge support from the IN-SYLVA network. We are grateful to the staff at the Itatinga Experimental Station, in particular Rildo Moreira e Moreira (Esalq, USP) and Eder Araujo da Silva (http://www.floragroapoio.com.br) for their technical support. This project analyses largely benefited from the Montpellier Bioinformatics Biodiversity (MBB) computing cluster platform which is a joint initiative of laboratories within the CeMEB LabEx "Mediterranean Center for Environment and Biodiversity", as part of the program "Investissements d'avenir" (ANR-10-LABX0004).

## 7. References

ABRAF, 2012. Chapter 01, Planted forests in Brazil. In, Statistical yearbook 2012.
Albaugh, T.J., Albaugh, J.M., Fox, T.R., Allen, H.L., Rubilar, R.A., Trichet, P., Loustau, D., Linder, S., 2016. Tamm Review: Light use efficiency and carbon storage in nutrient and water experiments on major forest plantation species. For Ecol Manag 376, 333-342.

Almeida, A.C., Landsberg, J.J., Sands, P.J., 2004. Parameterisation of 3-PG model for fast-growing Eucalyptus grandis plantations. For Ecol Manag 193, 179-195.
Aspinwall, M.J., Pfautsch, S., Tjoelker, M.G., Vårhammar, A., Possell, M., Drake, J.E., Reich, P.B., Tissue, D.T., Atkin, O.K., Rymer, P.D., Dennison, S., Van Sluyter, S.C., 2019. Range size and growth temperature influence Eucalyptus species responses to an experimental heatwave. Global Change Biology in press.
Battie-Laclau, P., Laclau, J.P., Domec, J.C., Christina, M., Bouillet, J.P., de Cassia Piccolo, M., de Moraes Goncalves, J.L., e Moreira, R.M., Krusche, A.V., Bouvet, J.M., Nouvellon, Y., 2014. Effects of potassium and sodium supply on drought-adaptive mechanisms in Eucalyptus grandis plantations. New Phytol 203, 401-413.
Bauerle, W.L., Bowden, J.D., McLeod, M.F., Toler, J.E., 2004. Modeling intra-crown and intra-canopy interactions in red maple: assessment of light transfer on carbon dioxide and water vapor exchange. Tree Physiol 24, 589-597.
Binkley, D., Campoe, O.C., Alvares, C., Carneiro, R.L., Cegatta, Í., Stape, J.L., 2017. The interactions of climate, spacing and genetics on clonal Eucalyptus plantations across Brazil and Uruguay. For Ecol Manag 405, 271-283.
Binkley, D., Laclau, J.-P., Sterba, H., 2013. Why one tree grows faster than another: Patterns of light use and light use efficiency at the scale of individual trees and stands. For Ecol Manag 288, 1-4.
Binkley, D., Stape, J.L., Bauerle, W.L., Ryan, M.G., 2010. Explaining growth of individual trees: Light interception and efficiency of light use by Eucalyptus at four sites in Brazil. For Ecol Manag 259, 17041713.

Bourdier, T., Cordonnier, T., Kunstler, G., Piedallu, C., Lagarrigues, G., Courbaud, B., 2016. Tree Size Inequality Reduces Forest Productivity: An Analysis Combining Inventory Data for Ten European Species and a Light Competition Model. Plos One 11, e0151852.
Campoe, O.C., Stape, J.L., Laclau, J.P., Marsden, C., Nouvellon, Y., 2012. Stand-level patterns of carbon fluxes and partitioning in a Eucalyptus grandis plantation across a gradient of productivity, in Sao Paulo State, Brazil. Tree Physiol 32, 696-706.
Campoe, O.C., Stape, J.L., Nouvellon, Y., Laclau, J.-P., Bauerle, W.L., Binkley, D., Le Maire, G., 2013. Stem production, light absorption and light use efficiency between dominant and non-dominant trees of Eucalyptus grandis across a productivity gradient in Brazil. For Ecol Manag 288, 14-20.
Charbonnier, F., le Maire, G., Dreyer, E., Casanoves, F., Christina, M., Dauzat, J., Eitel, J.U.H., Vaast, P., Vierling, L.A., Roupsard, O., 2013. Competition for light in heterogeneous canopies: Application of MAESTRA to a coffee (Coffea arabica L.) agroforestry system. Agric For Meteorol 181, 152-169.
Christina, M., Le Maire, G., Battie-Laclau, P., Nouvellon, Y., Bouillet, J.P., Jourdan, C., de Moraes Goncalves, J.L., Laclau, J.P., 2015. Measured and modeled interactive effects of potassium deficiency and water deficit on gross primary productivity and light-use efficiency in Eucalyptus grandis plantations. Global Change Biology 21, 2022-2039.
Christina, M., le Maire, G., Nouvellon, Y., Vezy, R., Bordon, B., Battie-Laclau, P., Gonçalves, J.L.M., Delgado-Rojas, J.S., Bouillet, J.P., Laclau, J.P., 2018. Simulating the effects of different potassium and water supply regimes on soil water content and water table depth over a rotation of a tropical Eucalyptus grandis plantation. For Ecol Manag 418, 4-14.
Christina, M., Nouvellon, Y., Laclau, J.-P., Stape, J.L., Bouillet, J.-P., Lambais, G.R., le Maire, G., 2017. Importance of deep water uptake in tropical eucalypt forest. Funct Ecol 31, 509-519.
Christina, M., Nouvellon, Y., Laclau, J.P., Stape, J.L., Campoe, O.C., le Maire, G., 2016. Sensitivity and uncertainty analysis of the carbon and water fluxes at the tree scale in Eucalyptus plantations using a metamodeling approach. Can J For Res 46, 297-309.
Cordonnier, T., Kunstler, G., 2015. The Gini index brings asymmetric competition to light. Perspectives in Plant Ecology, Evolution and Systematics 17, 107-115.

Crous, J., Burger, L., Sale, G., 2013. Growth response at age 10 years of five Eucalyptus genotypes planted at three densities on a drought-prone site in KwaZulu-Natal, South Africa. Southern Forests: a Journal of Forest Science 75, 189-198.
Dovey, S., Du Toit, B., 2006. Calibration of LAI-2000 canopy analyser with leaf area index in a young eucalypt stand.
Drake, J.E., Aspinwall, M.J., Pfautsch, S., Rymer, P.D., Reich, P.B., Smith, R.A., Crous, K.Y., Tissue, D.T., Ghannoum, O., Tjoelker, M.G., 2015. The capacity to cope with climate warming declines from temperate to tropical latitudes in two widely distributed Eucalyptus species. Global Change Biology 21, 459-472.
du Toit, B., 2008. Effects of site management on growth, biomass partitioning and light use efficiency in a young stand of Eucalyptus grandis in South Africa. For Ecol Manag 255, 2324-2336.
du Toit, B., Smith, C.W., Little, K.M., Boreham, G., Pallett, R.N., 2010. Intensive, site-specific silviculture: Manipulating resource availability at establishment for improved stand productivity. A review of South African research. For Ecol Manag 259, 1836-1845.
Elias, P., Boucher, D., 2014. Planting for the Future. How Demand for Wood Products Could Be Friendly to Tropical Forests. In. Union of Concerned Scientists.
Epron, D., Laclau, J.P., Almeida, J.C., Goncalves, J.L., Ponton, S., Sette, C.R., Jr., Delgado-Rojas, J.S., Bouillet, J.P., Nouvellon, Y., 2012. Do changes in carbon allocation account for the growth response to potassium and sodium applications in tropical Eucalyptus plantations? Tree Physiol 32, 667-679.
Epron, D., Nouvellon, Y., Mareschal, L., Moreira, R.M.e., Koutika, L.-S., Geneste, B., Delgado-Rojas, J.S., Laclau, J.-P., Sola, G., Gonçalves, J.L.d.M., Bouillet, J.-P., 2013. Partitioning of net primary production in Eucalyptus and Acacia stands and in mixed-species plantations: Two case-studies in contrasting tropical environments. For Ecol Manag 301, 102-111.
FAO, 2015. Global Forest Resources Assessment 2015.
Fernández-Tschieder, E., Binkley, D., 2018. Linking competition with Growth Dominance and production ecology. For Ecol Manag 414, 99-107.
Forrester, D.I., Ammer, C., Annighöfer, P.J., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Coll, L., del Río, M., Drössler, L., Heym, M., Hurt, V., Löf, M., den Ouden, J., Pach, M., Pereira, M.G., Plaga, B.N.E., Ponette, Q., Skrzyszewski, J., Sterba, H., Svoboda, M., Zlatanov, T.M., Pretzsch, H., 2018. Effects of crown architecture and stand structure on light absorption in mixed and monospecific Fagus sylvatica and Pinus sylvestris forests along a productivity and climate gradient through Europe. J Ecol 106, 746-760.
Gastellu-Etchegorry, J.P., Martin, E., Gascon, F., 2004. DART: a 3D model for simulating satellite images and studying surface radiation budget. Int J Remote Sens 25, 73-96.
Giardina, C.P., Ryan, M.G., Binkley, D., Fownes, J.H., 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Global Change Biology 9, 1438-1450.
Gonçalves, J.L.d.M., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., Ferraz, S.F.d.B., Lima, W.d.P., Brancalion, P.H.S., Hubner, A., Bouillet, J.-P.D., Laclau, J.-P., Nouvellon, Y., Epron, D., 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. For Ecol Manag 301, 6-27.
Gonçalves, J.L.M., Wichert, M.C.P., Gava, J.L., Masetto, A.V., Junior, A.J.C., Serrano, M.I.P., Mello, S.L.M., 2007. Soil fertility and growth of Eucalyptus grandis in Brazil under different residue management practices. Southern Hemisphere Forestry Journal 69, 95-102.
Gspaltl, M., Bauerle, W., Binkley, D., Sterba, H., 2013. Leaf area and light use efficiency patterns of Norway spruce under different thinning regimes and age classes. For Ecol Manag 288, 49-59.
Guillemot, J., Martin-StPaul, N.K., Dufrêne, E., François, C., Soudani, K., Ourcival, J.M., Delpierre, N., 2015. The dynamic of the annual carbon allocation to wood in European tree species is consistent with a combined source-sink limitation of growth: implications for modelling. Biogeosciences 12, 2773-2790.

Haynes, B.E., Gower, S.T., 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol 15, 317-325.
IBA, 2017. Brazilian Tree Industry Annual Report. https://www.iba.org/datafiles/publicacoes/pdf/ibarelatorioanual2017.pdf.
Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. For Ecol Manag 352, 920.

King, D.A., 1997. The Functional Significance of Leaf Angle in Eucalyptus. Aust J Bot 45, 619-639.
Laclau, J.P., Almeida, J.C., Goncalves, J.L., Saint-Andre, L., Ventura, M., Ranger, J., Moreira, R.M., Nouvellon, Y., 2009. Influence of nitrogen and potassium fertilization on leaf lifespan and allocation of above-ground growth in Eucalyptus plantations. Tree Physiol 29, 111-124.
Laclau, J.P., Bouillet, J.P., Goncalves, J.L.M., Silva, E.V., Jourdan, C., Cunha, M.C.S., Moreira, M.R., SaintAndre, L., Maquere, V., Nouvellon, Y., Ranger, J., 2008. Mixed-species plantations of Acacia mangium and Eucalyptus grandis in Brazil - 1. Growth dynamics and aboveground net primary production. For Ecol Manag 255, 3905-3917.
Landsberg, J.J., Hingston, F.J., 1996. Evaluating a simple radiation/dry matter conversion model using data from Eucalyptus globulus plantations in Western Australia. Tree Physiol 16, 801-808.
Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For Ecol Manag 95, 209-228.
le Maire, G., Marsden, C., Verhoef, W., Ponzoni, F.J., Lo Seen, D., Bégué, A., Stape, J.-L., Nouvellon, Y., 2011. Leaf area index estimation with MODIS reflectance time series and model inversion during full rotations of Eucalyptus plantations. Remote Sens Environ 115, 586-599.
le Maire, G., Nouvellon, Y., Christina, M., Ponzoni, F.J., Gonçalves, J.L.M., Bouillet, J.P., Laclau, J.P., 2013. Tree and stand light use efficiencies over a full rotation of single- and mixed-species Eucalyptus grandis and Acacia mangium plantations. For Ecol Manag 288, 31-42.
LI-Cor, I., 1992. LAI-2000 Plant Canopy Analzyer, Operating Manual. In. Lincoln, NE.
Li, W., Fang, H., 2015. Estimation of direct, diffuse, and total FPARs from Landsat surface reflectance data and ground-based estimates over six FLUXNET sites. Journal of Geophysical Research: Biogeosciences 120, 96-112.
Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems. Global Change Biology 13, 2089-2109.
Luu, T.C., Binkley, D., Stape, J.L., 2013. Neighborhood uniformity increases growth of individual Eucalyptus trees. For Ecol Manag 289, 90-97.
Luyssaert, S., Inglima, I., Jung, M., Richardson, A., Reichstein, M., Papale, D., Piao, S.L., Schulze, E.-D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K., Bonal, D., Bonnefond, J.M., Chambers, J.Q., Ciais, P., Cook, B., Davis, K.J., Dolman, A.J., Gielen, B., Goulden, M.L., Grace, J., Granier, A., Grelle, A., Griffis, T., GrÃ1⁄nwald, T., Guidolotti, G., Hanson, P.J., Harding, R., Hollinger, D.Y., Hutyra, L.R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B.E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E.J., Munger, J.W., Nikinmaa, E., Ollinger, S.V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M.J., Seufert, G., Sierra, C., Smith, L.K., Tang, J., Valentini, R., Vesala, T., Janssens, I.A., 2007. CO2 balance of boreal, temperate, and tropical forests derived from a global database. Global Change Biology 13, 2509-2537.
MacDicken, K.G., 2015. Global Forest Resources Assessment 2015: What, why and how? For Ecol Manag 352, 3-8.
Marsden, C., Le Maire, G., Stape, J.L., Lo Seen, D., Roupsard, O., Cabral, O., Epron, D., Nascimento Lima, A.M., Nouvellon, Y., 2010. Relating MODIS vegetation index time-series with structure, light
absorption and stem production of fast-growing Eucalyptus plantations. For Ecol Manag 259, 17411753.

Marsden, C., Nouvellon, Y., Laclau, J.-P., Corbeels, M., McMurtrie, R.E., Stape, J.L., Epron, D., le Maire, G., 2013. Modifying the G'DAY process-based model to simulate the spatial variability of Eucalyptus plantation growth on deep tropical soils. For Ecol Manag 301, 112-128.
Monteith, J.L., Moss, C.J., 1977. Climate and the Efficiency of Crop Production in Britain [and Discussion]. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 281, 277-294.
Nouvellon, Y., Begue, A., Moran, M.S., Lo Seen, D., Rambal, S., Luquet, D., Chehbouni, G., Inoue, Y., 2000. PAR extinction in shortgrass ecosystems: effects of clumping, sky conditions and soil albedo. Agric For Meteorol 105, 21-41.
Nouvellon, Y., Laclau, J.P., Epron, D., Le Maire, G., Bonnefond, J.M., Goncalves, J.L., Bouillet, J.P., 2012. Production and carbon allocation in monocultures and mixed-species plantations of Eucalyptus grandis and Acacia mangium in Brazil. Tree Physiol 32, 680-695.
Nouvellon, Y., Stape, J.L., Laclau, J.P., Bonnefond, J.M., Da Rocha, H.R., Campoe, O.C., Marsden, C., Bouillet, J.P., Loos, R.A., Kinana, A., Le Maire, G., Saint Andre, L., Roupsard , O., 2010. Water and energy fluxes above an Eucalyptus plantation in Brazil: environmental control and comparison with two eucalypt plantations in Congo. In, Sir Mark Oliphant Canopy Processes in a Changing Climate Conference (formally the IUFRO Canopy Processes Meeting), Falls Creek, Victoria and Tarraleah, Tasmania.
Nouvellon, Y., Stape, J.L., Le Maire, G., Bonnefond, J.-M., Guillemot, J., Christina, M., Bouillet, J.-P., Camargo Campoe, O., Laclau, J.-P., 2018. Full-rotation carbon, water and energy fluxes in a tropical eucalypt plantation. In, Eucalyptus 2018. CIRAD, Montpellier, France, pp. 102-103, 101 poster.
Oliveira, J.D.C., Feret, J.B., Ponzoni, F.J., Nouvellon, Y., Gastellu Etchegorry, J.-P., Camargo Campoe, O., Stape, J.L., Estraviz Rodriguez, L.C., Le Maire, G., 2017. Simulating the canopy reflectance of different eucalypt genotypes with the DART 3-D model. IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing 10, 4844-4852.
Pallett, R.N., Sale, G., 2004. The relative contributions of tree improvement and cultural practice toward productivity gains in Eucalyptus pulpwood stands. For Ecol Manag 193, 33-43.
Parveaud, C.-E., Chopard, J., Dauzat, J., Courbaud, B., Auclair, D., 2007. Modelling foliage characteristics in 3D tree crowns: influence on light interception and leaf irradiance. Trees 22, 87-104.
Payn, T., Carnus, J.-M., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., Orazio, C., Rodriguez, L., Silva, L.N., Wingfield, M.J., 2015. Changes in planted forests and future global implications. For Ecol Manag 352, 57-67.
Pérez-Cruzado, C., Muñoz-Sáez, F., Basurco, F., Riesco, G., Rodríguez-Soalleiro, R., 2011. Combining empirical models and the process-based model 3-PG to predict Eucalyptus nitens plantations growth in Spain. For Ecol Manag 262, 1067-1077.
Pfautsch, S., Harbusch, M., Wesolowski, A., Smith, R., Macfarlane, C., Tjoelker, M.G., Reich, P.B., Adams, M.A., 2016. Climate determines vascular traits in the ecologically diverse genus Eucalyptus. Ecol Lett 19, 240-248.
Pinheiro, R.C., de Deus, J.C., Nouvellon, Y., Campoe, O.C., Stape, J.L., Aló, L.L., Guerrini, I.A., Jourdan, C., Laclau, J.-P., 2016. A fast exploration of very deep soil layers by Eucalyptus seedlings and clones in Brazil. For Ecol Manag 366, 143-152.
Pinkard, E.A., Patel, V., Mohammed, C., 2006. Chlorophyll and nitrogen determination for plantationgrown Eucalyptus nitens and E. globulus using a non-destructive meter. For Ecol Manag 223, 211217.

Pirard, R., Dal Secco, L., Warman, R., 2016. Do timber plantations contribute to forest conservation? Environmental Science \& Policy 57, 122-130.

Posada, J.M., Lechowicz, M.J., Kitajima, K., 2009. Optimal photosynthetic use of light by tropical tree crowns achieved by adjustment of individual leaf angles and nitrogen content. Ann Bot-London 103, 795-805.
Rambal, S., Ourcival, J.-M., Joffre, R., Mouillot, F., Nouvellon, Y., Reichstein, M., Rocheteau, A., 2003. Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy. Global Change Biol 9, 1813-1824.
Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. J Ecol 102, 275-301.
Resende, R.T., Marcatti, G.E., Pinto, D.S., Takahashi, E.K., Cruz, C.D., Resende, M.D.V., 2016. Intragenotypic competition of Eucalyptus clones generated by environmental heterogeneity can optimize productivity in forest stands. For Ecol Manag 380, 50-58.
Resende, R.T., Soares, A.A.V., Forrester, D.I., Marcatti, G.E., dos Santos, A.R., Takahashi, E.K., e Silva, F.F., Grattapaglia, D., Resende, M.D.V., Leite, H.G., 2018. Environmental uniformity, site quality and tree competition interact to determine stand productivity of clonal Eucalyptus. For Ecol Manag 410, 7683.

Roupsard, O., Dauzat, J., Nouvellon, Y., Deveau, A., Feintrenie, L., Saint-André, L., Mialet-Serra, I., Braconnier, S., Bonnefond, J.-M., Berbigier, P., Epron, D., Jourdan, C., Navarro, M., Bouillet, J.-P., 2008. Cross-validating Sun-shade and 3D models of light absorption by a tree-crop canopy. Agric For Meteorol 148, 549-564.
Russell, G., Jarvis, P., Monteith, J., 1989. Absorption of radiation by canopies and stand growth. Plant canopies: their growth, form and function 31, 21-39.
Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecol Monogr 74, 393-414.
Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. Plant, Cell \& Environment 29, 367-381.
Ryan, M.G., Stape, J.L., Binkley, D., Fonseca, S., Loos, R.A., Takahashi, E.N., Silva, C.R., Silva, S.R., Hakamada, R.E., Ferreira, J.M., Lima, A.M.N., Gava, J.L., Leite, F.P., Andrade, H.B., Alves, J.M., Silva, G.G.C., 2010. Factors controlling Eucalyptus productivity: How water availability and stand structure alter production and carbon allocation. For Ecol Manag 259, 1695-1703.
Sands, P.J., Landsberg, J.J., 2002. Parameterisation of 3-PG for plantation grown Eucalyptus globulus. For Ecol Manag 163, 273-292.
Silva, P.H.M., Campoe, O.C., De Paula, R.C., Lee, D.J., 2016. Seedling Growth and Physiological Responses of Sixteen Eucalypt Taxa under Controlled Water Regime. Forests 7, 110.
Soares, A.A.V., Leite, H.G., Souza, A.L., Silva, S.R., Lourenço, H.M., Forrester, D.I., 2016. Increasing stand structural heterogeneity reduces productivity in Brazilian Eucalyptus monoclonal stands. For Ecol Manag 373, 26-32.
Stape, J.L., Binkley, D., 2010. Insights from full-rotation Nelder spacing trials with Eucalyptus in São Paulo, Brazil. Southern Forests: a Journal of Forest Science 72, 91-98.
Stape, J.L., Binkley, D., Ryan, M.G., 2008. Production and carbon allocation in a clonal Eucalyptus plantation with water and nutrient manipulations. For Ecol Manag 255, 920-930.
Stape, J.L., Binkley, D., Ryan, M.G., Fonseca, S., Loos, R.A., Takahashi, E.N., Silva, C.R., Silva, S.R., Hakamada, R.E., Ferreira, J.M.d.A., Lima, A.M.N., Gava, J.L., Leite, F.P., Andrade, H.B., Alves, J.M., Silva, G.G.C., Azevedo, M.R., 2010. The Brazil Eucalyptus Potential Productivity Project: Influence of water, nutrients and stand uniformity on wood production. For Ecol Manag 259, 1684-1694.
Vezy, R., Christina, M., Roupsard, O., Nouvellon, Y., Duursma, R., Medlyn, B., Soma, M., Charbonnier, F., Blitz-Frayret, C., Stape, J.-L., Laclau, J.-P., de Melo Virginio Filho, E., Bonnefond, J.-M., Rapidel, B., Do, F.C., Rocheteau, A., Picart, D., Borgonovo, C., Loustau, D., le Maire, G., 2018. Measuring and
modelling energy partitioning in canopies of varying complexity using MAESPA model. Agric For Meteorol 253-254, 203-217.
Vicca, S., Luyssaert, S., Peñuelas, J., Campioli, M., Chapin III, F.S., Ciais, P., Heinemeyer, A., Högberg, P., Kutsch, W.L., Law, B.E., Malhi, Y., Papale, D., Piao, S.L., Reichstein, M., Schulze, E.D., Janssens, I.A., 2012. Fertile forests produce biomass more efficiently. Ecol Lett 15, 520-526.

Wang, Y., Jarvis, P., Taylor, C., 1991. PAR absorption and its relation to above-ground dry matter production of Sitka spruce. J Appl Ecol, 547-560.
Whitehead, D., Beadle, C.L., 2004. Physiological regulation of productivity and water use in Eucalyptus: a review. For Ecol Manag 193, 113-140.
Will, R.E., Barron, G.A., Colter Burkes, E., Shiver, B., Teskey, R.O., 2001. Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of Pinus taeda and Pinus elliottii stands of different densities. For Ecol Manag 154, 155-163.




12


13


16

























Table 1: Description of the 16 genotypes. Climate (annual mean) values are from (Alvares et al., 2013). States: SP: são Paulo; ES: Espírito Santo; MG: Minas Gerais; BA: Bahia; RS: Rio Grande do Sul; Climate: Cfa: Humid subtropical zone without dry season and with hot summer; Cwa: Humid subtropical zone with dry winter and hot summer; Cfa: Humid subtropical zone without dry season and with hot summer; Aw: Tropical zone with dry winter; Am: Tropical zone - monsoon; Cwb: Humid subtropical zone with dry winter and temperate summer; As: Tropical zone with dry summer;

| Genotype | Species | Propagation | State of origin | Climate | Minimum temperature $\left({ }^{\circ} \mathrm{C}\right)$ | Maximum temeprature $\left({ }^{\circ} \mathrm{C}\right)$ | Mean annual temperature $\left({ }^{\circ} \mathrm{C}\right)$ | $\qquad$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | E. grandis | Seed | SP | Cfa | 15.9 | 22.5 | 19.7 | 1336 |
| 2 | E. grandis | Seed | SP | Cfa | 15.9 | 22.5 | 19.7 | 1336 |
| 3 | E. grandis x E. urophylla | Clone | SP | Cwa | 17.1 | 23.2 | 20.7 | 1463 |
| 4 | E. grandis x E. urophylla | Clone | SP | Cfa | 15.9 | 22.5 | 19.7 | 1336 |
| 5 | E. grandis x E. urophylla | Clone | SP | Cwa | 17.1 | 23.2 | 20.7 | 1463 |
| 6 | E. grandis x E. urophylla | Clone | ES | Aw | 20.2 | 26.1 | 23.4 | 1304 |
| 7 | E. grandis x E. urophylla | Clone | MG | Cwa | 17.9 | 22.9 | 21.1 | 1396 |
| 8 | E. grandis x E. urophylla | Clone | MG | Aw | 19.4 | 24.9 | 22.6 | 1370 |
| 9 | E. grandis x E. urophylla | Clone | BA | Am | 20.9 | 25.8 | 23.8 | 1192 |
| 10 | E. grandis x E. urophylla | Clone | SP | Cfa | 15.4 | 22.4 | 19.3 | 1245 |
| 11 | E. grandis x E. urophylla | Clone | SP | Cfa | 15.4 | 22.4 | 19.3 | 1245 |
| 12 | E. urophylla $x$ sp | Clone | MG | Cwb | 16.5 | 21.7 | 19.7 | 1180 |
| 13 | E. grandis x E. urophylla | Clone | MG | Cwb | 16.5 | 21.7 | 19.7 | 1180 |
| 14 | E. saligna | Clone | RS | Cfa | 13.2 | 24.2 | 18.4 | 1594 |
| 15 | E. grandis | Clone | SP | Cfa | 15.4 | 22.4 | 19.3 | 1245 |
| 16 | E. grandis x E. camaldulensis | Clone | BA | As | 22.4 | 26.1 | 24.7 | 1045 |

Alvares, A.C., Stape, J., Sentelhas, P., Gonçalves, J., Sparovek, G., 2013. Köppen's climate classification map for Brazil.

Table 2: Description of the measurements conducted in the experiment. Each number is a code described below the table, informing on the measured blocks and genotypes numbers. Other information such as the number of trees or leaves sampled are also given. DBH: trunk diameter at 1.3 m; Refl/Tran: reflectance/transmittance: LAI-2000: measurements with the LiCor PCA LAI-2000 device (see section 2.6).

| Date | age (years) | DBH | H | DBH <br> border t . | Biomass | Leaf angles | SPAD | Leaf Refl/Tran | LAI-2000 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 03/11/2009 | 0 |  |  |  |  |  |  |  |  |
| 17/05/2010 | 0.53 | 1 | 1 |  |  |  |  |  |  |
| 03/11/2010 | 1.00 | 1 | 1 |  | 5a | 6 | 7 | 7 |  |
| 01/06/2011 | 1.58 | 1 | 1 |  |  |  |  |  |  |
| 01/01/2012 | 2.16 | 1 | 1 |  |  |  |  |  |  |
| 01/06/2012 | 2.58 |  |  | 4 | 5a | 6 |  |  |  |
| 01/07/2012 | 2.66 | 3 | 3 |  |  |  |  |  |  |
| 15/01/2013 | 3.20 | 1 | 2 |  |  |  |  |  |  |
| 15/07/2013 | 3.70 | 3 | 3 |  |  |  |  |  |  |
| 15/11/2013 | 4.04 |  |  |  | 6 b | 6 b |  |  |  |
| 15/02/2014 | 4.29 | 1 | 2 |  |  |  |  |  |  |
| 15/06/2014 | 4.62 |  |  |  |  |  |  |  | 9 |
| 23/06/2014 | 4.64 | 3 | 3 | 4 | 5b | 6 | 8 |  |  |
| 31/10/2014 | 5.00 | 3 b | 3 b |  |  |  |  |  |  |
| 15/02/2015 | 5.28 | 1 | 2 |  |  |  |  |  |  |
| 15/07/2015 | 5.70 | 3 | 3 |  |  |  |  |  |  |
| 15/11/2015 | 6.03 |  |  |  | 5b | 6 | 7 | 7 |  |
| 15/01/2016 | 6.20 | 1 | 2 |  |  |  |  |  |  |
| 1: all blocks; all genotypes; all inside plot trees |  |  |  |  |  | 6: B2 B3 B10; all genotypes; 12 trees/genotype; 60 leaves/tree 6b: B2 B3 B10; G1 G6 G8 G12 G14 G16; 12 trees/genotype; 60 |  |  |  |
| 2: all blocks; all genotypes; 24 inside plot trees/genotype |  |  |  |  |  | leaves/tree |  |  |  |
| 3: B3 B8 B10; G1 G6 G8 G12 G14 G16; all inside plot trees |  |  |  |  |  | 7: B1 B2; all genotypes; 3 trees/genotype; 6 leaves/tree |  |  |  |
| 3b: B3 B8 B10; G1 G6 G8 G12 G14 G16; 24 inside plot trees/genotype |  |  |  |  |  | 8: B2 B3 B10; all genotypes; 3 trees/genotype; 6 leaves/tree |  |  |  |
| 4: all blocks; all genotypes; all border trees |  |  |  |  |  | 9: B2 B3 B8; all genotypes; 12 positions/genotype |  |  |  |
| 5a: B1 B2 B4 B5 B6 B7 B9 ; all genotypes; 6-12 trees/genotype |  |  |  |  |  |  |  |  |  |
| 5b: B2 B3 B8 B10 ; all genotypes; 6-12 trees/genotype |  |  |  |  |  |  |  |  |  |

Table 3: Result of mixed model of fAPAR in function of plot averages characteristics, with all genotypes included and with the blocks considered as random effect. One model was adjusted each year. Some variables, noted "o", were first removed after computing their Variance Inflation Factors (VIF), to solve multicollinearity issue (see Section 2.7). Then, a backward elimination of nonsignificant effects of the linear mixed effects model was performed (eliminated variables are noted " x "). Remaining significant variables are labelled with $* * *$ if $\mathrm{p}<0.001, * * \mathrm{p}<0.01, * \mathrm{p}<0.05$ of the Ftest of the fixed effects, green if the effect on fAPAR is positive and red if the effect is negative

| Age | 1 | 2 | 3 | 4 | 5 | 6 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| LAI | $* * *$ | $* * *$ | $* * *$ | $* * *$ | $* * *$ | $* * *$ |
| LIA | $* * *$ | $* * *$ | $* * *$ | $* * *$ | o | o |
| Reflectance | x | $*$ | x | o | x | $*$ |
| Transmitance | x | x | $*$ | x | $* * *$ | $* * *$ |
| SPAD | o | $* * *$ | x | x | $* * *$ | x |
| Crown height | o | o | o | o | o | o |
| Crown diameter | $* * *$ | o | o | o | $* * *$ | $* * *$ |
| Crown volume | o | $* * *$ | x | x | o | o |
| Crown ratio | o | x | $*$ | $* *$ | $*$ | $*$ |
| Trunk biomass | x | $* * *$ | o | x | o | x |
| H | $* * *$ | o | $* * *$ | $* * *$ | $* * *$ | $* * *$ |
| DBH | o | o | x | o | $*$ | $* *$ |
| GINI | x | x | o | o | o | o |
| Mortality | x | x | x | $* * *$ | x | x |

