



Stem production, light absorption and light use efficiency between dominant and non-dominant trees of *Eucalyptus grandis* across a productivity gradient in Brazil

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ABSTRACT

Brazilian *Eucalyptus* plantations are some of the most productive forest plantations in the world, sustaining mean growth rates of 25 Mg ha⁻¹ year⁻¹ (50 m³ ha⁻¹ year⁻¹) over the 4.7 million hectares planted across the country. To better understand forest productivity, studies at the stand scale need to be coupled with tree level evaluations of the production ecology (the assessment of wood production as a function of crown light absorption and light use efficiency). The soil clay content (≈20% to ≈40%), topography and historical land use of the experimental site generated a natural gradient in productivity. We measured (from 6 to 7 years after planting) stem wood dry biomass growth and estimated light absorption and light use efficiency at the tree level with a three-dimensional array model (MAESTRA) in 12 plots within a seed-origin *Eucalyptus grandis* plantation. We investigated the hypothesis that dominant trees (the 20% largest) are more productive than non-dominant trees (the 20% smallest) as a result of greater light absorption and light use efficiency; and that with increasing productivity across plots, dominant trees would show larger increases in light use and light use efficiency in comparison to non-dominant trees. The 20% smallest of the trees averaged 10.6 kg of stem wood dry biomass (1.6 kg of stem wood growth during the last year of the rotation), compared with 185 kg per stem wood in the 20% largest of trees (34 kg of stem wood growth over the same period). The smallest trees contained 7.2% of the leaf area as compared to the largest trees (3.0 m² versus 41.7 m²), and they absorbed only 6.7% as much light (2.2 versus 32.8 GJ year⁻¹). The smallest trees grew at about 4.7% of the rate of the largest trees, which is a smaller percentage than the difference in absorbed photosynthetically active radiation; therefore the light use efficiency was lower for the smallest trees (0.75 kg GJ⁻¹ versus 1.03 kg GJ⁻¹). Our results show the significant contribution of dominant trees to stand productivity and the importance of evaluating production ecology at the individual tree scale.

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1. Introduction

The forestry sector in Brazil has dramatically increased the productivity of exotic *Eucalyptus* plantations through intensive silviculture, genetic selection and breeding techniques (Gonçalves et al., 2004, 2008; Stape et al., 2010). Currently, most of the 4.7 million hectares are located in northeastern and southeastern Brazil, and are used for charcoal production, pulp, processed and solid

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wood. Silvicultural systems now yield an average of 20–25 Mg ha⁻¹ year⁻¹, typical for clonal plantations (ABRAF, 2011). The high yields in clonal plantations result not only from superior genetics and silviculture, but also from the uniform structure that develops in clonal stands (Binkley et al., 2002; Boyden et al., 2008).

The uniformity achieved through intensive exploitation of genotypes may be limited by the spatial variability of resources (water, nutrients and solar radiation), which leads to heterogeneity in tree growth and reductions in productivity at stand and landscape levels (Ryan et al., 2010; Stape et al., 2010; Aspinwall et al., 2011). For example, Stape et al. (2010) found that plantations with moderate to high heterogeneity of tree sizes (with uniform genetics, silviculture and spacing) yielded 5–20% less wood growth

per hectare than highly uniform stands. The reduction in productivity was attributed to a high dominance in heterogeneous populations, because the efficiency of resource use declined for non-dominant trees (Boyden et al., 2008; Binkley et al., 2010).

Based on the production ecology theory, the productivity of a forest can be represented quantitatively as a function of the availability of resources (notably water, nutrients and solar radiation) and the resource use rate and efficiency from which trees produce wood and non-woody tissue (Cannell, 1989; Binkley et al., 2004). Over time, the growth of individual trees changes in response to competition-related differences in resource acquisition and efficiency of resource use (Binkley et al., 2004; Doi et al., 2010).

The size of a tree affects its ability to absorb available resources, the efficiency of resource conversion into biomass, and the partitioning of biomass into wood growth. Christina et al. (2011) found almost symmetrical growth rates above and below ground in intensively managed *Eucalyptus* plantations, suggesting that larger trees have a greater potential to explore their environment, as compared to smaller trees. Dominant trees have higher rates of resource acquisition than non-dominant trees, and they typically use the resource as efficiently, or more efficiently, than non-dominant trees (Binkley et al., 2013; Le Maire et al., 2013). These differences in resource use and efficiency between dominant and non-dominant trees are enhanced and more evident on sites with higher resources availability (Campoe et al., 2013a). Higher efficiency may relate to greater total biomass production, or to greater biomass partitioning in wood.

We used the production ecology approach to examine patterns in growth, light use, and light use efficiency at an individual tree level across a 90 ha stand of seed-origin *Eucalyptus grandis* in the state of São Paulo. The plot-level wood productivity of this stand differed by more than 50% as a result of differences in soil physical and chemical attributes (Campoe et al., 2012b). We hypothesized that within plots, dominant trees are more productive than non-dominant trees as a result of greater light absorption and light use efficiency (wood growth/light absorption). We also hypothesized that with increasing productivity across plots, dominant trees would show larger increases in light use and light use efficiency in comparison to non-dominant trees.

2. Site description and methods

2.1. Study site

The study site is located in the southeast of Brazil, in São Paulo State, at 22°58'04"S, 48°43'40"W, in a 90 ha plantation of *E. grandis* managed by Duratex company. Since the establishment of the stand, the mean annual rainfall is 1277 mm, with 75% concentrated from October to March. During the study period, from October 2008 to September 2009, cumulated rainfall was 29% higher (1646 mm). Mean annual temperature was 19.2 °C, ranging from 13.3 °C (June to August) to 27.2 °C (December to February). The mean annual air relative humidity was 77%, with minimum values during winter months (~45%).

Soils are deep oxisols (Silva et al. 2011) developed on cretaceous sandstone in the upper part of the study site (750 m above sea level) and basaltic material at the lowest elevation (725 m above sea level).

The study site was planted in December 2002 with *E. grandis* (W. Hill ex Maiden) seedlings from a 2nd generation seed orchard (Coff's Harbour – Australia provenance) following minimum cultivation techniques of site preparation (Gonçalves et al., 2004). Trees were spaced at 3.75 m × 1.60 m (1666 trees per hectare). Rows were oriented East–West and positioned between stumps of the previous 12-year *Eucalyptus* rotation (approximately 900 stumps ha⁻¹). Stump densities were variable across the study area and the yield

of the current rotation was generally higher in the areas with the lowest tree stocking density before 2002. The historical land use within the study area, in complement with the topography and soil clay content, influenced the productivity of the current rotation (Campoe et al., 2012b). Glyphosate was used (4 L ha⁻¹) to eliminate competing vegetation prior to site preparation and until canopy closure (approximately 18 months after planting). Leaf cutting ants (*Atta* sp. and *Acromyrmex* sp.) were controlled using sulfluramide-based baits whenever necessary.

Fertilizers and Lime were applied up to the 3rd year, totaling 62 kg N ha⁻¹, 26 kg P ha⁻¹, 97 kg K ha⁻¹, 300 kg Ca ha⁻¹, 144 kg Mg ha⁻¹, 11 kg S ha⁻¹, 2.4 kg B ha⁻¹, 1.6 kg Zn ha⁻¹ and 1.3 kg Cu ha⁻¹.

2.2. Experimental design and tree growth

The diameters (*D*, 1.3 m above ground level) were measured on all trees in the 90 ha stand (~145,000 measured trees) during February of 2008. This complete census was used to choose 12 plots spanning the range of stand productivity. Each plot contained 6 rows of 14 trees/row (84 trees, ~504 m²), with stem dry biomass ranging from 122 Mg ha⁻¹ to 187 Mg ha⁻¹ at 6 years old. Plots with elevation ranging from 726 m to 731 m were located on soils with

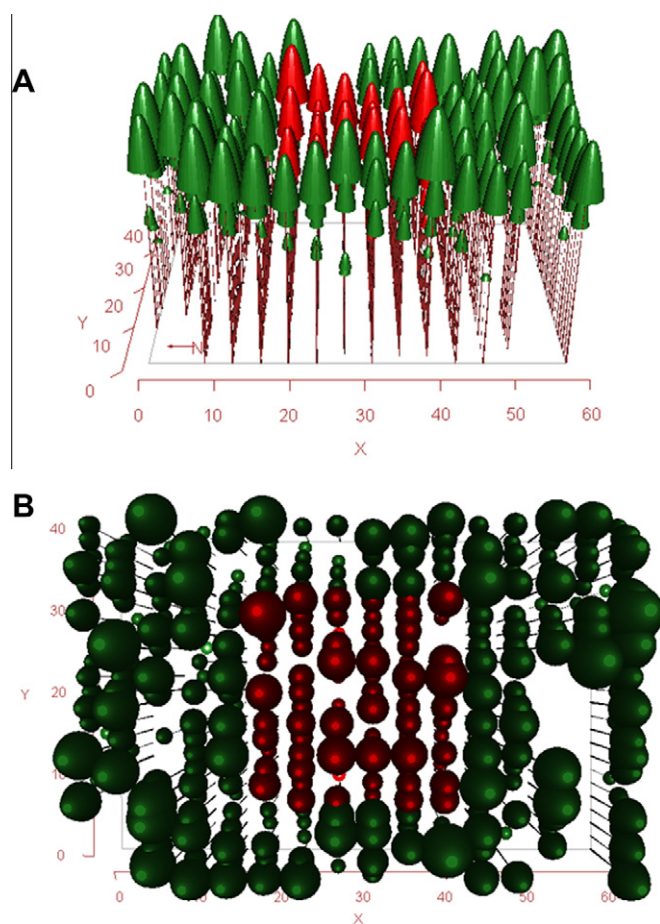


Fig. 1. Schematic representation (in scale) of the positioning and size of trees present in plot 1 with elevation of 726 m (A: frontal view, B: orthogonal view). The red crown trees are the focal trees used in MAESTRA simulations, and the outer five rows of green crown trees were included in the simulation only for their potential shading on focal trees. This figure was made using the Maeswrap package in R (R. Duursma, <http://cran.r-project.org/web/packages/Maeswrap/index.html>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

high clay content ($\approx 40\%$) and plots from 740 m to 756 m were located on soils with low clay content ($\approx 20\%$).

Tree growth on the 12 plots was assessed by measuring bole circumference (C , 1.3 m above ground level) and total height (H) of all trees at the beginning (late September 2008) and end (late September 2009) of the study period. Stem dry biomass growth was estimated by applying local-specific dry biomass equations on D and H measurements over the study period. Equation fitting and maximum likelihood estimation was performed using PROC NLP in SAS (SAS Institute, Cary, NC, USA) (Saint-André et al., 2005). See Campoe et al. (2012b) for the complete description of the stem dry biomass equation development.

2.3. MAESTRA parameterization

Radiation absorption for each tree was simulated with MAESTRA (Wang and Jarvis, 1990; Medlyn, 2004; Bauerle et al., 2004), a three dimensional ecophysiological model that estimates radiation absorption, photosynthesis and transpiration at the individual tree level. MAESTRA accounts for the influence of shading from leaves within a crown and by those of neighboring crowns. From destructive sampling ($n = 40$), we measured tree crown structural characteristics to parameterize MAESTRA (Campoe, 2012). Height to the base of the live crown and crown radius in four directions for all trees on the 12 plots were estimated based on these allometric equations (Campoe, 2012). Individual tree leaf area ($m^2 tree^{-1}$) was calculated from allometric equations, based on D and H (Nouvellon et al., 2010), assuming homogeneous distribution on vertical and horizontal directions. We used two local-specific equations due to differences in topography and soil physical and chemical attributes (Campoe, 2012).

Due to significant seasonal changes in tree leaf area over the year (decrease during dry season and increase in wet season), we used the dynamics leaf area index obtained from MODIS time-series images of our study site over the study period, to estimate tree leaf area variation (Le Maire et al., 2011). Each tree leaf area, estimated at date t_{ref} from allometric equations, was multiplied by the ratio of current MODIS LAI divided by the MODIS LAI at t_{ref} as was done in le Maire et al. (2013). A MODIS pixel covers an area of ~ 5.3 ha and is representative of the local LAI dynamics of the plots. The assumption that all tree leaf areas varied in the same manner and proportionally to their size is coherent with other results obtained in *Eucalyptus* plantations (Le Maire et al., 2011). Leaf inclination angle was measured on 20 leaves per crown third on 40 destructively sampled trees, assuming half-ellipsoidal crown shape (Campbell and Norman, 1998). We used the average leaf inclination angle for the three crown thirds of 59.6° (based on horizontal plane).

Soil reflectance and leaf reflectance and transmittance were estimated in the visible and near infrared spectra with an ASD Field SpecPro (Analytical Spectral Devices, Boulder, Colorado, USA) spectrometer and an ASD leaf-clip probe in *Eucalyptus* plantations in the State of São Paulo, with similar age, silvicultural management and fertilization regime (Le Maire et al., 2013). We used 0.067 for soil reflectance, and 0.048 for reflectance and 0.034 for transmittance of the leaves.

The incident photosynthetically active radiation (PAR) was measured at 30-min intervals using the BF3 sensor (Delta-T Devices, Burwell, Cambridge, UK) mounted on a weather station in the middle of the experimental area. The positioning of trees in the plots followed an x, y grid and was based on a tree spacing of 3.75×1.60 m between plants and rows (Fig. 1). The slope was $< 2\%$ within each plot and the methodology of Norman and Welles (1983) was used to account for the scattering of radiation, the proportion of direct and diffuse radiant energy and position of the sun. The MAESTRA model calculated absorbed PAR (APAR) at 30-min

Table 1 Mean biometric values per tree for the 20% smallest, overall average and 20% largest of trees in each plot 6 years after planting. Crown radius A is perpendicular to planting rows and crown radius B is parallel to planting rows. Number of trees per plot considered at the beginning of the study period.

Plot number	Plot elevation m	Trees per plot	20% Smallest						Average						20% Largest							
			D		H		Crown length		Crown radius A		Crown radius B		D		H		Crown length		Crown radius A		Crown radius B	
			cm	m	m	m	m	m	m	m	m	m	cm	m	m	m	m	m	m	m	m	m
1	726	77	8.5	16.0	2.0	0.8	0.9	0.9	1.3	1.2	16.1	26.8	6.3	1.3	1.2	22.4	32.7	7.9	1.9	1.6		
2	727	81	4.6	9.3	0.8	0.8	0.8	1.2	1.2	14.3	23.9	5.2	1.2	1.2	22.3	32.4	7.7	1.9	1.6			
3	730	81	6.1	12.2	1.3	0.8	0.9	1.3	1.3	15.2	25.0	5.4	1.3	1.2	21.9	32.2	7.7	1.8	1.5			
4	731	71	5.6	11.9	0.9	0.8	0.9	1.3	1.3	15.5	25.3	5.4	1.3	1.2	23.2	32.3	7.1	2.0	1.6			
5	740	79	9.0	17.7	2.5	0.9	0.9	1.3	1.2	15.4	26.2	6.0	1.3	1.2	21.0	31.9	7.9	1.7	1.5			
6	746	78	7.6	15.7	1.6	0.8	0.9	1.4	1.1	14.7	25.5	5.8	1.2	1.1	20.8	30.9	7.1	1.7	1.4			
7	747	81	7.1	14.9	1.7	0.9	0.9	1.4	1.2	13.2	22.2	5.0	1.4	1.2	18.8	26.7	6.8	2.0	1.7			
8	755	78	6.2	14.1	1.4	0.8	0.8	1.4	1.3	13.3	23.2	6.0	1.4	1.3	19.1	27.8	7.9	2.1	1.8			
9	755	78	6.0	13.2	1.2	0.8	0.8	1.5	1.5	13.5	23.4	6.2	1.5	1.3	18.8	28.2	8.3	2.1	1.8			
10	756	76	6.0	13.3	1.1	0.8	0.8	1.4	1.3	13.4	22.8	5.6	1.4	1.3	19.5	27.8	7.8	2.2	1.8			
11	756	77	6.4	14.3	2.1	0.9	0.9	1.5	1.5	13.6	23.7	6.4	1.5	1.3	18.4	28.0	8.3	2.0	1.7			
12	756	72	4.6	10.3	0.9	0.8	0.8	1.2	1.2	13.4	22.6	4.3	1.2	1.1	22.2	30.4	5.9	1.8	1.5			
Average	744	77	6.5	13.6	1.5	0.8	0.9	1.3	1.3	14.3	24.2	5.6	1.3	1.2	20.7	30.1	7.5	1.9	1.6			

intervals for each m² of leaf area throughout the crown of each tree.

Light absorption was modeled for all the trees in each plot, with five surrounding rows of buffer trees (Fig. 1). The path length of radiation penetrating each crown took into consideration the distribution of leaf area and leaf angles along the crown. The direct and diffuse radiation were treated separately, and the transmission of diffuse PAR was modeled by the method of Norman (1979).

The light use efficiency (LUE, kg GJ⁻¹) was calculated as stem dry biomass production from each target tree (kg tree⁻¹yr⁻¹) divided by the APAR (GJ tree⁻¹ yr⁻¹). The influence of tree size (based on stem wood dry biomass) on light absorption and light use efficiency was examined by comparing the 20% smallest of trees, the average tree, and the 20% largest of trees in each plot.

The aim of our study was whole crown light absorption; therefore we held MAESTRA leaf-level photosynthesis and stomatal conductance parameters constant and evaluated the effect of dominance on stem growth, APAR and LUE by ranking all the trees from small to large based on stem wood dry biomass. We examined the observed patterns by fitting linear or exponential functions and used significance value (*P*-value), coefficient of determination (*R*²) and root mean square error (RMSE) to select the best fitted models (Sigmaplot 10, SPSS, 2010).

3. Results

The seedling-origin trees showed large variation in size within each plot. Diameter showed an average coefficient of variation (CV) of 36% and *H* showed 26% (Table 1). Live crown length was more variable, with an average CV of 47%. Across all plots, trees averaged 14.3 cm in *D*, 24.2 m in *H*, with 5.6 m of crown length and crown radii of 1.2 m (parallel planting rows) and 1.3 m (perpendicular to planting rows). The 20% smallest of the trees averaged 6.5 cm in *D*, with *H* of 13.6 m and crown radii of 0.85 m. In contrast, the 20% largest of the trees averaged 20.7 cm in *D*, 30.1 m in *H*, and 1.6–1.9 m in crown radius (parallel and perpendicular to planting rows, respectively).

The average stem wood biomass per tree ranged from 69 kg to 115 kg (6 years after planting) and the stem wood growth from 12 kg year⁻¹ to 18 kg year⁻¹ from 6 to 7 years after planting (Table 2). These differences in tree sizes and stem wood production were also evident in the crowns, with average leaf area ranging from 16 m² tree⁻¹ to 23 m² tree⁻¹ among plots. Differences in mean APAR (21% between contrasting plots) per tree were smaller than differences in leaf area (44% between contrasting plots) among plots (Table 2), ranging from 12.2 GJ APAR year⁻¹ to 14.8 GJ APAR year⁻¹.

The trees comprising the 20% smallest of the population averaged 10.6 kg of stem wood biomass (1.6 kg of stem wood growth in the last year of the rotation), compared with 185 kg of stem in the 20% largest of the population (34 kg of stem wood growth over the same period). The smallest trees supported 7.2% of the leaf area as that carried by the largest trees (3.0 m² tree⁻¹ versus 41.7 m² tree⁻¹), and they absorbed only 6.7% as much light (2.2 versus 32.8 GJ tree⁻¹ year⁻¹). The smallest trees grew at about 4.7% of the rate of the largest trees, which is a smaller percentage than the difference in APAR; therefore the light use efficiency was 37% lower for the smallest trees (0.75 kg GJ⁻¹ versus 1.03 kg GJ⁻¹). These patterns of APAR and LUE in relation to tree size support our hypothesis.

Light absorption increased exponentially with increasing tree leaf area (Fig. 2). Given that larger trees had greater leaf area, stem wood growth (Fig. 3A and C) and light absorption (Fig. 3B and D) increased exponentially with tree size and with tree rank

Table 2 Stem wood dry biomass (6 years after planting) and growth, leaf area, absorbed photosynthetically active radiation (APAR), and light use efficiency (LUE = stem wood dry biomass growth per APAR) for small (20% smallest), overall average and large (20% largest) trees in each plot, from 6 to 7 years after planting.

Plot number	Plot elevation m	20% Smallest				Average				20% Largest					
		Stem wood kg	Stem growth kg year ⁻¹	Leaf area m ²	APAR GJ year ⁻¹	Stem wood kg	Stem growth kg year ⁻¹	Leaf area m ²	APAR GJ year ⁻¹	LUE kg GJ ⁻¹	Stem wood kg	Stem growth kg year ⁻¹	Leaf area m ²	APAR GJ year ⁻¹	LUE kg GJ ⁻¹
1	726	19.5	3.3	4.1	2.9	115.3	18.3	20.9	14.6	1.26	225.9	42.6	42.9	36.1	1.18
2	727	3.9	0.7	2.3	2.2	97.6	15.3	19.1	13.5	1.14	223.2	41.5	45.0	36.2	1.15
3	730	7.2	1.1	2.6	2.4	106.0	14.8	20.3	12.9	1.14	211.8	33.8	41.5	30.4	1.11
4	731	6.7	0.9	2.6	2.3	113.2	16.6	21.8	14.8	1.12	241.6	42.5	48.4	37.0	1.15
5	740	22.4	3.3	4.5	3.1	100.1	16.3	18.2	13.1	1.25	193.7	37.1	36.5	30.8	1.20
6	746	14.4	2.1	4.1	3.0	93.1	14.9	20.5	13.8	1.08	183.9	34.2	41.6	30.2	1.13
7	747	12.2	1.9	2.8	1.7	68.6	11.6	16.2	12.2	0.95	138.9	26.0	35.0	30.6	0.85
8	755	9.3	1.3	2.3	1.5	74.8	13.0	17.9	13.5	0.97	150.2	28.4	38.1	32.0	0.89
9	755	7.9	1.4	2.5	1.5	78.9	14.2	23.4	14.6	0.97	146.3	27.8	45.4	30.8	0.90
10	756	8.1	1.3	2.0	1.4	76.3	13.4	18.0	13.6	0.99	156.0	30.6	39.1	35.1	0.87
11	756	12.2	1.5	2.8	1.7	78.2	14.2	17.8	13.7	1.03	139.2	27.0	33.3	28.6	0.94
12	756	4.0	0.6	3.0	2.6	81.8	12.9	20.8	13.4	0.97	207.9	36.3	54.0	35.9	1.01
Average	744	10.6	1.6	3.0	2.2	90.3	14.6	19.6	13.6	1.07	184.9	34.0	41.7	32.8	1.03

Table 3
Description of the relationships between tree stem wood biomass and tree stem wood growth and absorbed photosynthetically active radiation (APAR); and between tree stem biomass rank and tree stem wood biomass growth and APAR. *P*-values for all models were <0.0001.

Independent variable	Independent variable	Model	y0	a	b	RMSE	R ²
Stem wood biomass	Stem wood growth	$Y = a \cdot X^b$	–	0.062	1.199	3.808	0.91
	APAR	$Y = y0 + a \cdot X^b$	0.649	0.048	1.228	4.642	0.86
Tree biomass ranking	Stem wood growth	$Y = y0 + a \cdot X^b$	2.002	0.0013	2.258	4.633	0.87
	APAR	$Y = y0 + a \cdot X^b$	2.211	0.0009	2.323	5.031	0.83

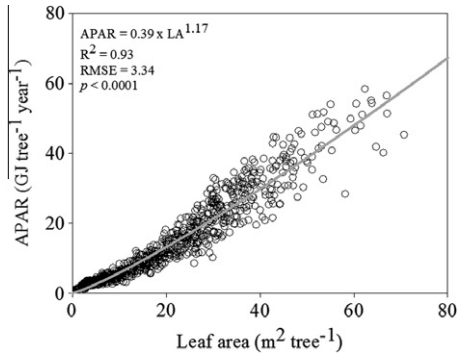


Fig. 2. Absorbed photosynthetically active radiation (APAR) as a function of leaf area for trees of all plots of the experimental area.

within the stand. Averaging by plot, higher growth rates showed higher light absorption and stem wood growth increased with increasing light interception across all size classes of trees. Higher growth rates also showed greater LUE, and the effect of LUE on growth rate was higher for small trees than for large trees (Fig. 4).

4. Discussion

Several studies on different tree species have found a positive linear relationship between leaf area and light absorption. Binkley

et al. (2010) found the relationship in clonal plantations of *Eucalyptus* in Brazil at mid-rotation (1.5–2.5 years old) and late-rotation (5.5–6.5 years old). Forrester et al. (2013) studying young (3.2 years) *Eucalyptus nitens* plantations in Australia, reported a linear slope, but it was different for thinned versus unthinned and pruned versus unpruned trees. Le Maire et al. (2013) showed increase in APAR on pure *Eucalyptus grandis* stands, on pure *Acacia mangium* stands and on mixed-plantations with these two species. Gspaltl et al. (2013) found a very strong relationship ($R^2 = 0.97–0.99$) between leaf area and APAR for Norway spruce (*Picea abies*) under different thinning regimes and age classes. The same linear pattern was observed on a young Loblolly pine (*Pinus taeda*) plantation in the USA, under different levels of irrigation and fertilization (Campoe et al., 2013a). Similar to our results, Binkley et al. (2002) also found an exponential relationship for seed-origin *Eucalyptus saligna* plantations in Hawaii. In all of these studies, large trees with more leaf area did not experience significant self-shading, as additional leaf area was displayed on crowns with a wider radius (see Binkley et al., 2013). This may be a general pattern among species, stand age, and silvicultural management.

The general trend of increasing LUE with increasing tree size was consistent across all of these studies, with the exception of Forrester et al. (2013), where there was no trend between LUE and tree size. In our study across a productivity gradient, on average dominant trees (20% largest) showed 37% greater LUE than suppressed trees (20% smallest). We know of no study that found

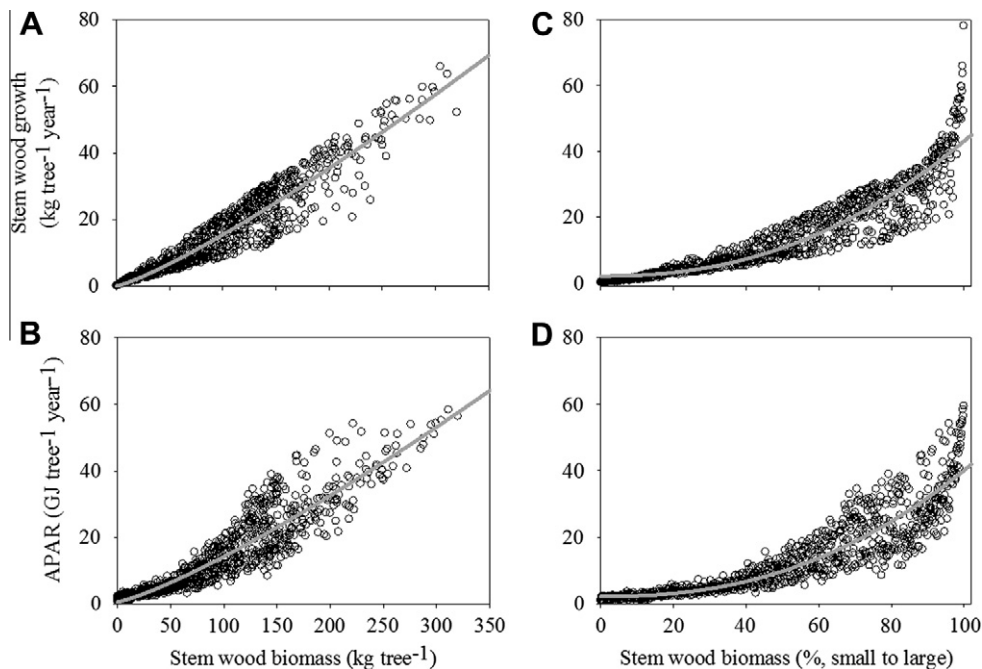


Fig. 3. Stem wood dry biomass growth and absorbed photosynthetically active radiation (APAR) as a function of tree stem wood dry biomass (A and B), and as a function of tree ranking (C and D) for all trees and plots. The pattern of increasing stem growth and APAR with larger or high ranking trees was consistent among the 12 plots. See Table 3 for the information of the relationships. See Table 3 for the relationships between presented variables.

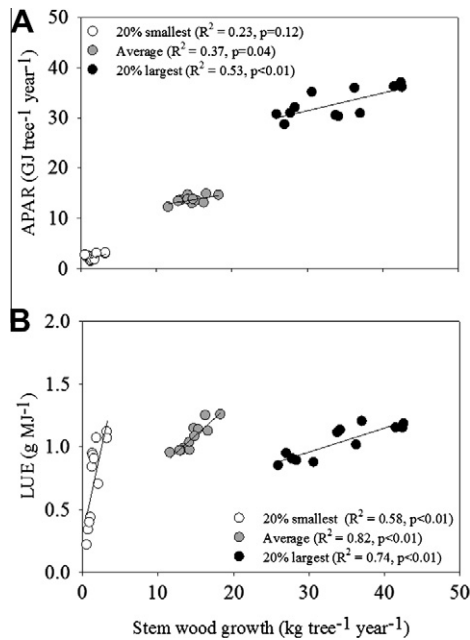


Fig. 4. Averaging by plot, higher growth rates showed higher light absorption (A). Higher growth rates also showed greater efficiency of light use (B), and the difference in efficiency was much stronger for small trees than for medium and large trees.

an opposite pattern of declining LUE with increasing tree dominance.

The differences in APAR and LUE between dominant and non-dominant trees are consistent and become larger on more productive plots. This pattern was also observed by Campoe et al. (2013a) on a Loblolly pine (*Pinus taeda*) plantation in the USA, where the differences in APAR and LUE between dominant and non-dominant trees were larger on irrigated and fertilized. These results suggest that dominant trees will become even more dominant over suppressed trees on sites with higher resource availabilities.

At the stand level, higher LUE in more productive stands might result from a greater rate of photosynthesis per unit APAR, or from increased partitioning of carbohydrates to stem growth (Giardina et al., 2003; Stape et al., 2008; O'Grady et al., 2010; Ryan et al., 2010; Campoe et al., 2012b). We suspect a shift in partitioning is important, but the difficulty of assessing belowground partitioning at the scale of individual trees leaves us uncertain about the relative contributions of photosynthesis versus altered partitioning in explaining the higher LUE of dominant trees.

The pattern of a strong dominance effect on LUE is consistent with the idea that high variation in stem sizes within plantations lowers stand growth, as a result of a greater proportion of absorbed light being used less efficiently by non-dominant trees (Binkley et al., 2010). What accounts for the initial development of dominance among trees within a stand? Potential factors include: (i) high quality seedlings tolerant to environmental stresses at the time of planting; (ii) microsite differences in soil fertility (either naturally or as a result of silvicultural operations) leading to variable resource availability, and (iii) variability in weed control, leading to competition for resources with invasive plants, mainly aggressive C_3 grasses (Nilsson and Allen, 2003; Gonçalves et al., 2008; Stape et al., 2010). Genotypic variation among seedlings may also be important due to different inherent growth potential (Aspinwall et al., 2011). In Brazil, silvicultural activities are the same for either clonal or seed grown *Eucalyptus* plantations. However, field experience shows that soil preparation (mainly depth), fertilizer distribution and weed control are heterogeneous at oper-

ational scale. This heterogeneity generates variation in resource availability creating dominance among trees within the stand. These factors affect the early development of trees before canopy closure, and then the pattern of dominance is well established and will intensify through the rotation (Binkley et al., 2004). High-precision silviculture operations and techniques may lead to high rates of production in part by enhancing uniformity within stands.

Future studies should focus on understanding the impact of tree dominance on planted forest productivity. Investigation of whole crown competition for resources at the tree level is needed to understand the dynamics of forest productivity at the landscape scale.

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