Forest Ecology and Management 466 (2020) 118125

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Influence of stand density on growth and water use efficiency in *Eucalyptus* clones

Rodrigo Eiji Hakamada[a,*], Robert M. Hubbard[b], Gabriela Gonçalves Moreira[c], Jose Luiz Stape[d], Otavio Campoe[e], Silvio Frosini de Barros Ferraz[c]

[a] Department of Forest Science, Federal Rural University of Pernambuco, Recife, PE 51.020-240, Brazil
[b] USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80526, United States
[c] Department of Forest Sciences, University of São Paulo, Piracicaba, SP 13.400-000, Brazil
[d] UNESP-FCA, Botucatu, SP CEP 18.610-300, Brazil
[e] Department of Forest Sciences, Federal University of Lavras, Lavras, MG 37200-000, Brazil

ARTICLE INFO

Keywords:
Transpiration
Water use efficiency
Planting density
Stocking
Clonal plantations

ABSTRACT

We examined the influence of stand density and genotype on transpiration and water use efficiency in high productivity plantations. Three widely planted *Eucalyptus* clones that differ in drought tolerance and productivity (*E. urophylla*, *E. urophylla* × *E. grandis* and *E. grandis* × *E. camaldulensis,* clones IP, B2 and C3, respectively) were measured at four densities (590, 1030, 1420, and 2950 trees ha^{-1}). Over the 1-year study period (1.5–2.5 years after planting), individual biomass increment decreased with increasing density, from 21 kg $tree^{-1}$ at 590 trees ha^{-1} to 6 kg $tree^{-1}$ at 2950 trees ha^{-1}. Stand increment typically follows the reverse pattern, increasing as density increases. This was the case for two clones (IP and B2), but stand increment was consistent across tree spacings for C3. Transpiration increased with density, from a low of 622 mm yr^{-1} to a high of 879 mm y^{-1}. Some of the increased water use resulted from higher leaf area index at higher densities. The B2 clone transpired the most water on average, produced the greatest increment (23 Mg ha^{-1} yr^{-1} for 1030 trees ha^{-1}), and produced the most wood L^{-1} transpiration (water use efficiency, 2.3 g biomass L^{-1}). The clone C3 had the lowest increment (only 12 Mg ha^{-1} yr^{-1}) because of the combination of low transpiration and low water use efficiency (only 1.5 g biomass L^{-1}). Optimizing clone selection and silviculture for the combination of high yield and high water use efficiency may help reduce risks from drought as well as water conservation.

1. Introduction

High productivity plantations account for about one-third of the global non-fuelwood supply, and the importance of plantations will increase as global wood demand rises to 9000 million m^3 yr^{-1} by 2050 (INDUFOR, 2012). The productivity of *Eucalyptus* plantations in Brazil increased about 4-fold over the past 50 years (Binkley et al., 2017), with a current average of 41 m^3 ha^{-1} yr^{-1} (ABRAF, 2013). As productivity increases, there is a need to understand how gains in wood production influence other resources, particularly water.

Water loss through transpiration is an inevitable consequence of photosynthetic carbon gain, and transpiration rates are typically greater in high productivity forests (Stape et al., 2004). Many studies have focused on the influence of superior genotypes and silvicultural practices on increased productivity and water use efficiency (Myers et al., 1996; Li, 2000; Albaugh et al., 2013; Otto et al., 2014) but the consequences of genotypic selection and silviculture on plantation water use remain largely unexplored. Water availability is typically the main limiting growth factor for operational *Eucalyptus* plantations in Brazil (Ryan et al., 2010; Stape et al., 2010), so better insights into water use and water use efficiency should be valuable.

Silvicultural practices that increase forest growth typically increase the efficiency of water use (Hubbard et al., 2010; Battie-Laclau et al., 2016). For example, fertilization increases light interception, photosynthesis, and partitioning of photosynthates to stemwood growth, with growth increases typically exceeding any increase in water use (Whitehead and Beadle, 2004). The overall effect on stand growth and ecosystem water balances depends on the relative sizes of increases in water use and water use efficiency, with implications for whole-catchment water budgets (Falkenmark and Rockstrom, 2006). Severe drought events in Brazil have become more frequent in recent years and have significantly increased the dry season in some regions (Booth,

* Corresponding author.
E-mail address: robert.hubbard@usda.gov (R.E. Hakamada).

https://doi.org/10.1016/j.foreco.2020.118125
Received 16 January 2020; Received in revised form 23 March 2020; Accepted 27 March 2020
Available online 06 April 2020
0378-1127/ Published by Elsevier B.V.

2013), so water consumption, drought tolerance, and water use efficiency have become increasingly important in silviculture (Vanclay, 2009; Ferraz et al., 2013; White et al., 2009).

We evaluated the effect of planting density of three clonal *Eucalyptus* genotypes that differ in drought sensitivity. We examined how difference in biomass increment developed from the interactions of clonal differences in water use and water use efficiency. From a practical point of view, we hope this work can identify interactions between genotypes and planting densities that may result in a reduction of water use without significantly impacting timber production.

2. Methods

2.1. Site description

The field experimental trees were planted in February 2012 near the city of Mogi Guacu (22°20′58″S, 46°58′16″W) in the northeast region of the state of São Paulo, Brazil. The site is part of the TECHS experimental network (Tolerance of Clonal *Eucalyptus* to Hydric and Thermal Stress; http://www.ipef.br/techs). A detailed description of the TECHS project can be found in Binkley et al. (2017), as well as other papers in this special issue.

The local climate is humid mesothermal (Cwa) according to the Köppen classification (Alvares et al., 2013). Elevation is 660 m with a mean annual temperature of 22 °C, with a minimum and maximum of 16 and 30 °C, and average mean annual precipitation of 1200 mm (Binkley et al., this issue). A prolonged dry period is important, with the 6-month period of April through September receiving only 20% of annual rain. At a regional scale, potential evapotranspiration exceeds rainfall by about 50 mm (Thornthwaite-Mather water balance model). The soil in the experimental area is a very deep (> 5 m) homogeneous Oxisol, with 38% clay in the 0–30 cm layer and a water storage capacity of 150 mm (Demattê, 2000). The area has been planted with *Eucalyptus* for about 50 years, and the previous 7-year rotation harvested in July 2011 had a mean annual increment of 55 m^3 ha^{-1} yr^{-1}.

We investigated growth, water use, and water use efficiency from 18 to 30 months after planting, near the time of peak growth in the rotation. The mean temperature for this period matched the long-term average of 22 °C, but rainfall (883 mm) was only 75% of average. The water deficit for the year was about 224 mm. The earlier months of the period were also below average in rainfall (Fig. 1), with total rainfall from planting through 30 months falling about 20% below the long-term average.

2.2. Experimental design

We examined three widely planted clonal genotypes that differ in drought *E. urophylla* × *grandis* (clone B2, low drought tolerance; *E. urophylla* (clone IP, moderate drought tolerance), and *E. grandis* × *E. camaldulensis* (clone C3, high drought tolerance, Eldridge et al., 1993; Gonçalves et al., 2013). We used a systematic plot design similar to Neldeŕs proposal (1962) in which tree spacing is constant within rows, but increased sequentially (Fig. 2). The spacing within rows was a constant 3.0 m, and between rows ranged from (from 0.25 m to 7.15 m, or ~13,000 trees ha^{-1} to ~450 trees ha^{-1}). We selected four densities, with row spacings of 1.1 m, 2.3 m, 3.2 m, and 5.6 m (2950, 1420, 1030 and 590 trees ha^{-1}, (Fig. 2). The selected range corresponds to the most commonly used planting densities for *Eucalyptus* plantations in Brazil (Gonçalves et al., 2013). Timber production for saw timber typically employs lower densities (< 600 plants ha^{-1}), with densities from 1000 to 1500 trees ha^{-1} for pulp and charcoal production, with densities > 2000 trees ha^{-1} for bioenergy production.

The unit of observation was the individual tree, with eight replicate trees for each clone × density treatment combination (96 measurement trees; 3 clones × 8 trees × 4 planting densities). One plot was planted for each clone and the area occupied by the three genotypes was 0.55 ha.

The soil was prepared using a minimum cultivation system (Gonçalves et al., 2013), with 60-cm deep subsoiling every three meters along rows. Nutritional limitations were eliminated by supplementing with 70 kg N ha^{-1}, 110 kg P ha^{-1}, and 160 kg K ha^{-1}. Micronutrients were applied as fritted trace elements. The area was kept completely free of pests, diseases (visually), and weed competition from the time the seedlings were planted. Ants were treated with ant bait consisting of 0.3% sulfluramide. Weeds were completely controlled with glyphosate herbicide at a dose of 2.88 kg active ingredient ha^{-1}. We guaranteed survival of 100% of the plantation by replanting less than 1% of the seedlings up to 30 days after the initial planting, in order to avoid artifacts in the regression analyses (Oda et al., 2008).

2.3. Measurements

2.3.1. Growth rate

We quantified stem growth rate with measurements every three months, from August 2013 to July 2014, of height and diameter at breast height (DBH) measured 1.3 m above ground level. We measured eight trees per planting density per clone. Based on the DBH and total

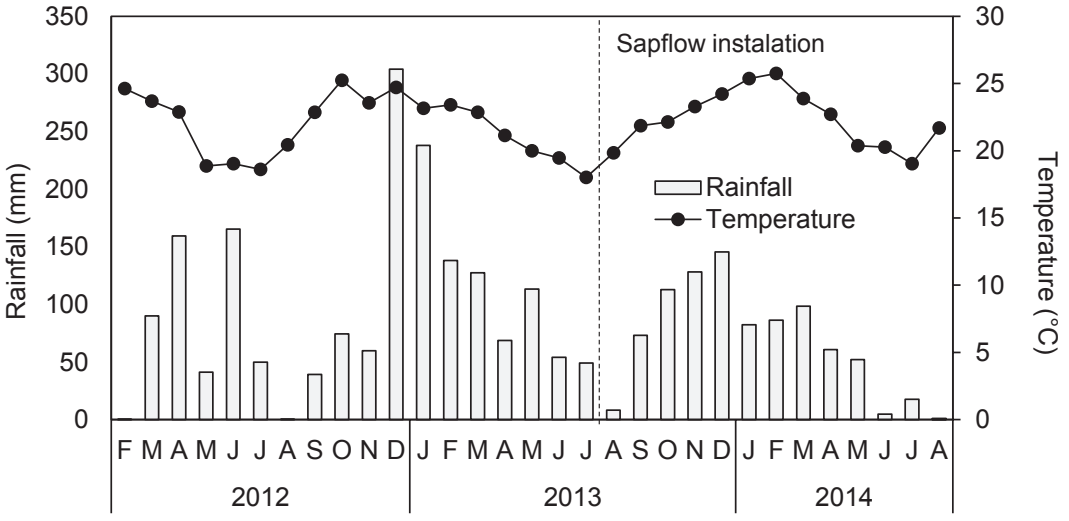

Fig. 1. Rainfall (mm) (bars) and average monthly temperatures (°C) (lines) of the *Eucalyptus* plantation site during the 2.5 years of tree growth. The vertical dotted line indicates the beginning of sapflow measurements.

Fig. 2. Schematic sketch of one clone density plot with seven rows and 27 plants per row. In each spacing evaluated (3.4, 7.0, 9.7 and 16.9 m^2 $tree^{-1}$), we measured eight trees. Sapflow was estimated with Granier-type heat probes insulated with reflective foil.

height values, we estimated the individual volume of each tree using the Schumacher and Hall (1933) model (Eq. (1)).

$$\text{Individual volume } (m^3 \text{ tree}^{-1}) = Exp^{-10.083+1.908*\ln(DAP)+1.031*\ln(H)} \quad (1)$$

Individual biomass was calculated by multiplying the volume by the basic density obtained in an adjacent site planted with an identical design to allow destructive samplings of eight trees per clone (unpublished data). The tree-level biomass estimates (t $tree^{-1}$) were used to estimate total stand biomass per hectare (t ha^{-1}) based on ground area available per tree.

2.3.2. Transpiration and water use efficiency

Transpiration was measured using 2-cm thermal dissipation sapflow probes (Granier, 1987). Sapflow density was calculated using a *Eucalyptus* specific calibration equation (Hubbard et al., 2010). Sapwood area was estimated using allometric equations based on diameter at breast height from 18 harvested trees from the adjacent site with identical planting densities. Thin (1–1.5 cm) disks were cut at breast height and conducting sapwood area was estimated visually by measuring four equally opposed radii of the obvious translucent portion of the disk and calculating area as an ellipse. Sapwood area in relation to DBH was estimated by power models for each clone (sapwood = a + b^{DBH}, $R^2 > 0.78$). Sapwood thickness ranged from 1.9 to 2.1 cm so we assumed the measured sap velocity by the probes was representative of the entire sapwood conducting area. Individual transpiration (L $tree^{-1}$) was estimated as the product of sapflow density and sapwood area. Data were collected every 15 s, and the average was recorded every 15 min via a multiplexer coupled to a data logger (CR1000 and AM 16/32, Campbell Scientific, Inc., Logan, UT). To minimize the variance in sap velocity associated with circumference, we initially positioned probes randomly at each cardinal position (north, south, east, and west), and moved the sensors 90° clockwise every three months (Grime and Sinclair, 1999). Styrofoam and foil backed insulation were used to minimize the influence thermal gradients and solar radiation at the measurement point and plastic bags were placed around the insulation to protect probes against moisture and stemflow (Fig. 2). Total stand transpiration (mm ha^{-1}) was estimated from the eight individual transpiration values obtained per plot. Seasonal water use efficiency (dry period considered the sum of August to October 2013 and May to August 2014-33% of yearly rainfall - and wet period from November to April 2014–66% of yearly rainfall) (WUE, g biomass L^{-1} transpired H_2O) was calculated as the ratio between the increases in wood biomass and transpiration.

2.3.3. Leaf area index

Light (photosynthetically active radiation, PAR) interception was measured with an LP-80 ceptometer (Decagon Devices Inc., Pullman, WA, USA) at plantation ages of 18, 22, 25, and 30 months. We conducted two transects per spacing, with 16 measurement locations per transect. For each plot, we also took a measurement outside the canopy during the measurement period. Measurements were taken from 11:30 to 13:00 on cloudless days with no wind interference that influence our measurements (Breda, 2003). PAR readings inside and outside the canopy were averaged individually, and Beer's law was used to estimate LAI, assuming a coefficient of light extinction (K) of 0.5, which has been widely used in tropical *Eucalyptus* plantations (Almeida et al., 2004; Mattos et al., this issue).

2.3.4. Statistical analysis

Data were analyzed using linear and nonlinear regressions, with planting density as the independent variable and dependent variables of leaf area index, tree biomass, individual transpiration, extrapolated stand biomass, stand transpiration and efficiency of water use. We used CurveExpert version 2.6 (http://www.curveexpert.net/) to find the best fit based on the minimal Akaike Information Criterion (AIC) value and higher coefficient of determination (r^2). We also used non-linear regression to calculate sapwood area relative to the diameter at breast height (DBH) for each clone. Significance was assessed at $\alpha = 0.05$. We performed homogeneity of variance and normality tests for all regressions to verify that the data had equal variance and were normally distributed. Analysis of variance followed by Tukeý's test was performed to compare stand biomass increment, transpiration, and water use efficiency between the three clones at the 1420 trees ha^{-1} planting density. Data were analyzed using Sigma Plot software (Systat Software, San Jose, CA, USA).

3. Results

3.1. Leaf area index

Leaf area index (LAI) varied among clones but increased with planting density for all clones (Fig. 3). The clone C3 had the lowest LAI, which is characteristic of the *E. camaldulensis* species. Clones B2 and IP had higher values, ranging from about 2.5 in the lowest density plots to 4.5 in the highest.

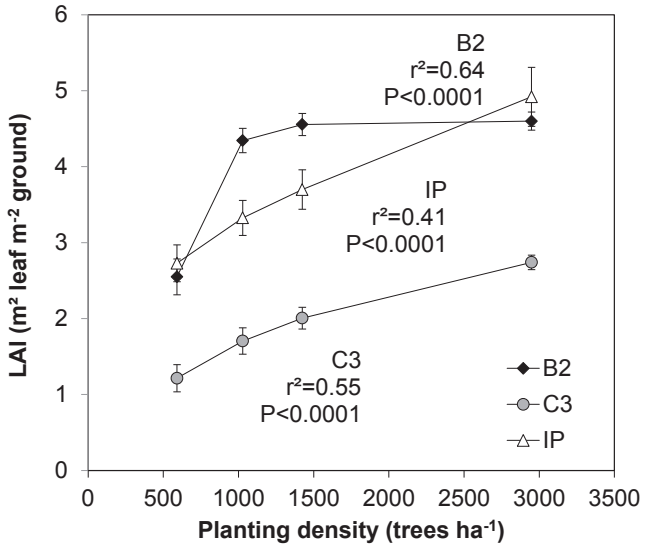

Fig. 3. Leaf area index as affected by planting density as the average of four measurements taken over the 1-year evaluation period (1.5–2.5 years after planting). Error bars represent standard error of the mean of four measurements within the period. All models are presented in Table 1.

3.2. Individual biomass and transpiration

The biomass of individual trees declined with density for all three clones (Fig. 4A) for all three clones. The average increment of trees for the three clones at the lowest density (590 trees ha^{-1}) was 21 kg $tree^{-1}$ (ranging from 19 to 23 kg $tree^{-1}$) compared with only 6 kg $tree^{-1}$ (from 4 to 8 kg $tree^{-1}$) at the highest density (2950 trees ha^{-1}). Individual transpiration followed the same trend with trees at the lowest density transpiring 29 L $tree^{-1}$ day^{-1} (ranging from 26 to 31 L $tree^{-1}$ day^{-1}) and those at the highest density only 8 L $tree^{-1}$ day^{-1} (from 7.6 to 10.0 L $tree^{-1}$ day^{-1}) (Fig. 4B).

3.3. Stand increment, transpiration, and water use efficiency during the dry and rainy seasons

Planting density affected both growth and transpiration and had mixed effects across clones and seasons. Stand biomass (scaled from individual tree measurements) increased with increasing planting density for the B2 and IP clones in both the dry and wet seasons as well as for the full year of evaluation. In contrast, stand biomass of the clone C3 did not show a significant increase during the study period (Fig. 5A, B, C). Stand transpiration remained stable for all planting densities and clones (Fig. 5D) in the dry season. However, during the rainy season and over the entire year, transpiration increased with increasing plant density (Fig. 5E, F). Mean transpiration in the 590 trees ha^{-1} treatment (averaged over all three clones) was 622 mm (ranging from 567 to 656 mm), which was 40% lower than that exhibited by the 2950 trees ha^{-1} treatment (879 mm, varying from 785 to 1047 mm). The greatest difference between clones occurred in the densest treatment: the clone IP had a transpiration rate of 785 mm, 25% lower than that of B2 (1047 mm) (Fig. 5F). Planting density did not affect the WUE of IP or B2 (Fig. 5G-I), whereas the clone C3 had a slight reduction in WUE at high planting densities, albeit only during the rainy season.

4. Discussion

There was a significant interaction between the clones and density on biomass, transpiration and water use efficiency. Stand biomass and transpiration increased proportionally with planting density for two of the three clones, giving constant water use efficiency for two clones. The drought tolerant clone C3 showed no increase in stand increment with density, and showed a slight decline in water use efficiency with increasing density only during the rainy season. Because water use efficiency differed between clones at each planting density, there may be opportunities to select clonal material and silvicultural treatments that maximize productivity while minimizing stand water use.

There was a decrease in individual biomass increment and an increase in stand biomass increment with increasing density, as commonly found in spacing trials (Schönau and Coetzee, 1989; Stape and Binkley, 2010; Forrester et al., 2013). The increment in light capture resulting from increased LAI partially explains the greater increase in stand biomass increment that occurred in denser treatments (Landsberg and Waring, 1997). The increase in LAI was associated with an increase in stand transpiration, but this pattern was not consistent across the clones and densities. The transpiration rate of the C3 clone was 8% higher than that of the IP clone, but the C3 clone's LAI was 78% lower (Fig. 3). Nogueira (2014) analyzed the anatomical characteristics of 16 genotypes of *Eucalyptus* and found that the clone C3 had the highest stomatal area, with stomata occurring on both adaxial and abaxial surfaces. This characteristic may explain C3's higher transpiration rate and lower LAI.

Planted forests with a focus on stand wood biomass have been managed in rotations of 5–10 years without thinning, especially in regions of high production potential (Gonçalves et al., 2008). Most studies that have examined density effects on transpiration have used

Table 1
Parameters and fitting statistics for leaf area index, individual biomass increment and individual transpiration models for clones *E. grandis* × *E. urophylla* (B2), *E. grandis* × *E. camaldulensis* (C3) and *E. urophylla* (IP).

Clone	Model	Parameter				Fitting statistics		
		b0	b1	b2	b3	R^2	P-value	AIC
B2	$LAI = b0 - (b1 * exp^{(-b2*Stocking)^{b3}}$	4.59	43.9	−0.00081	−0.93	0.64	< 0.0001	−54
	$Individual\ \ biomass\ \ increment = b0 * exp^{\frac{b1}{Stocking}}$	0.0065	684.6			0.91	< 0.0001	−396
	$Individual\ \ transpiration = \frac{1}{b0 + b1 * ln(Stocking)}$	−0.198	0.0371			0.90	< 0.0001	112
C3	$LAI = \frac{b0 * stocking}{b1 + stocking}$	4.008	1384			0.55	< 0.0001	−65
	$Individual\ \ biomass\ \ increment = b0 * stocking^{b1}$	15.90	−1.057			0.84	< 0.0001	−386
	$Individual\ \ transpiration = b0 * stocking^{b1}$	8203	−0.877			0.87	< 0.0001	88
IP	$LAI = b0 * stocking^{b1}$	0.59	0.367			0.41	< 0.0001	−2
	$Individual\ \ biomass\ \ increment = b0 * exp^{\frac{b1}{Stocking}}$	0.0048	915.2			0.86	< 0.0001	−387
	$Individual\ \ transpiration = b0 * stocking^{b1}$	1375	−0.964			0.87	< 0.0001	79

AIC: Akaike Information Criterion.

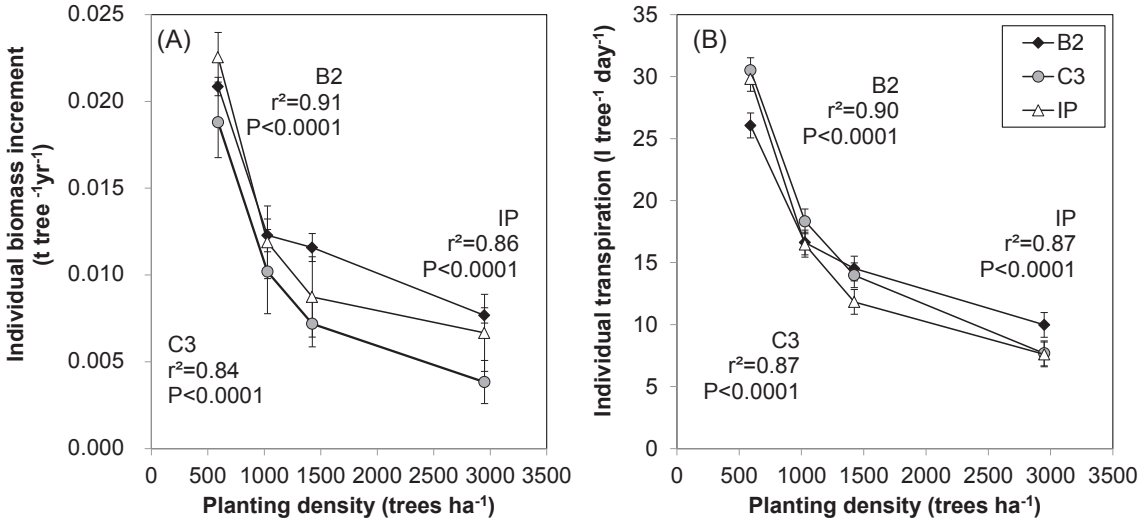

Fig. 4. (A) Individual biomass increment (t tree^{-1} yr^{-1}) over 12 months (1.5–2.5 years after planting) and (B) average individual transpiration (L tree^{-1} day^{-1}) as affected by plant density for the B2, C3, and IP clones. Error bars represent standard error of the mean of eight trees. All models are presented in Table 1.

density levels generated by thinning rather than planting (Stoneman et al., 1996; Lesch and Scott, 1997; Forrester et al., 2012). Importantly, controlling planting density by thinning may have a different effect than when density is defined during planting (Whitehead et al., 1984). In a study evaluating the effect of planting density on water consumption in seed origin *Eucalyptus tereticornis*, Kallarackal and Somen, 1997) obtained transpiration results similar to ours, with a 45% decrease in transpiration observed when planting density was reduced from 1800 to 1090 plants ha^{-1}.

Differences in water use efficiency were very important between clones, but not for density. White et al. (2014) showed similar results where WUE did not change when an *E. globulus* plantation grown from seed was thinned from 1200 to 300 stems ha^{-1}. Using the clone C3 at 1420 plants ha^{-1} as a reference (a common density for *Eucalyptus* plantations, Gonçalves et al., 2013), there are significant differences between clones regarding biomass increment, transpiration, and WUE (Fig. 6). Relative to C3, the B2 clone had 45% more biomass increment and 61% higher water use efficiency (Fig. 6A, C) but no increase in transpiration (Fig. 6B). On the other hand, the clone IP did not show an increase in biomass (Fig. 6D) but had a 16% lower transpiration rate (Fig. 6E), thereby increasing WUE by 44% (Fig. 6F).

Why did the most drought tolerant clone present the lowest WUE? Hybrid genotypes may have characteristics of the species that gave rise to the material (Zobel et al., 1987). Therefore, it is possible that drought-tolerant plants have high water consumption at the same time, characteristics that can be inherited from different species. In the present case, clone C3, which has a high tolerance to drought, probably acquired from the species *E. camaldulensis*, also had a high transpiration, probably originated from the crossing with *E. grandis*. Many studies can be explained by several characteristics studied for the same material in Brazil. Clone C3 has a high total belowground carbon flux (TBCF), allocating 47% of Gross Primary Production (GPP) to belowground, about 10% more than clone B2 at the same site (Campoe et al., this issue). Genotypes with low LAI such as C3 tend to have higher root area index to leaf area index ratio (Pinheiro et al., 2016), and normally has a very deep fine root system compared to genotypes that are less drought tolerant (Reis et al., 2006; Pinheiro et al., 2016). It helps to confirm that C3 invests more carbon in roots, improving this strategy to avoid drought negative effects. Hamer et al. (2016) showed eucalypt species naturally from drier sites has a higher root to leaf area ratio, as could be a strategy to support dry periods (Laclau et al., 2013; Christina et al., 2018). The C3 clone is also amphistomatous (stomata on adaxial and abaxial leaf surfaces) (Otto et al., 2017) which could lead to greater transpiration rates per leaf area.

As population pressures increase and climate change driven extreme drought events become more frequent, there is a critical need for a more integrative approach to managing water resources that includes participation of downstream stakeholders. Our data from the three clones we measured illustrate the potential of clonal selection and as a tool to manage water use within the plantation. For example, choosing B2 in relation to the clone C3, would increase not only productivity, but also WUE, while transpiration remains unchanged (Fig. 6). This strategy could be indicated for areas without conflicts over water use. Conversely, in areas with water use conflicts, managers might choose the IP clone as opposed to C3. This choice leads to decreased transpiration but maintains productivity by choosing a more water use efficient clone.

A potential limitation of our study is the lack of replication within and across sites. Although we report results for only one site and one year of assessment, the patterns of physiological responses of the three clones followed similar trends. Therefore, we believe that trees planted at different times and in different locations would exhibit trends similar to those observed in the present study. The experimental site is uniform, but small differences in the soil could have influenced the physiology of the trees and there could be competitive influences from adjacent plots. However, we expect that a fourfold difference in planting density would have a greater impact on tree physiology than small variations in soil properties or competitive influences. Furthermore, the patterns of increased stand biomass and leaf area with increasing density were consistent for multiple clones and across all of the TECHS sites. Given the tight relationship between productivity and leaf area, we suggest our results are likely applicable to other *Eucalyptus* plantations within Brazil.

Increased timber production will always be the main objective of forest plantation management. However, there is a growing societal demand for plantations that utilize adaptive management to protect and preserve downstream resources. This study suggests that there may be alternatives to increase biomass increment that can occur concomitantly with water conservation values. We suggest that future studies address clonal selection, planting density and water use efficiency in regions with prolonged periods of drought in order to better understand the effect of such conditions on water use by plantations and downstream water delivery.

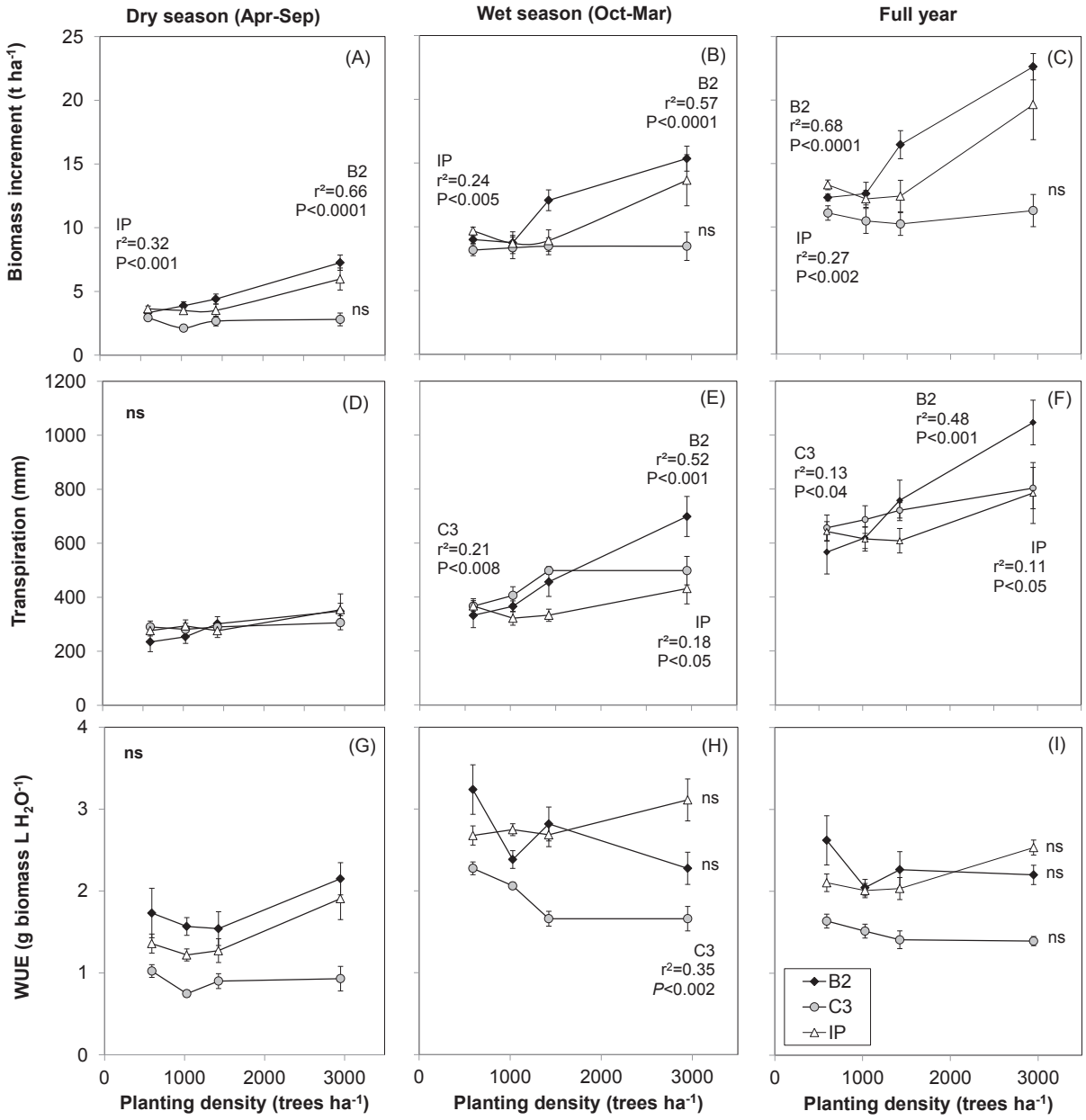

Fig. 5. Increased planting density resulted in increased biomass (A, B, C) and transpiration (D, E, F); however, it did not affect water use efficiency (G, H, I), regardless of whether the evaluation period was the full year (18 to 30 months after planting) or the dry or wet seasons. Error bars represent standard error of the mean. ns: not significant. All models are presented in Table 2.

CRediT authorship contribution statement

Rodrigo Eiji Hakamada: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing - original draft, Writing - review & editing. **Robert M. Hubbard:** Conceptualization, Investigation, Methodology, Resources, Supervision, Writing - review & editing. **Gabriela Gonçalves Moreira:** Data curation, Funding acquisition, Project administration, Resources. **Jose Luiz Stape:** Conceptualization, Writing - review & editing. **Otavio Campoe:** Funding acquisition, Writing - review & editing. **Silvio Frosini de Barros Ferraz:** Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the staff of International Paper, particularly Luis Fernando Silva, Adriano Almeida, Benedito Brandão, Ivan Balcão, and Gabriela Pires. We thank Dan Binkley and the TECHS group (Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses) for helpful discussions and experimental design support. The project was possible only through the coordination provided by Forestry Science and Research Institute (IPEF, ipef.br/techs/en, Directors Luiz Ernesto George Barrichelo and José Otávio Brito). TECHS was funded by the following 26 companies: Anglo American (Andre Machado), Arauco (Rodrigo Coutinho), Arborgen (Gabriela Bassa), ArcelorMittal (Roosevelt Almado), Cenibra (Fernando Leite), CMPC (Elias

Table 2
Models correlating wood growth (B), transpiration (T) and water use efficiency (WUE) and planting spacing (m^2 $tree^{-1}$) for hybrid clones of *E. urophylla* × *E. grandis* (B2), *E. grandis* × *E. camaldulensis* (C3) and *E. urophylla* (IP).

Genotype	Variable	Season	Model	R^2	*E*	AIC
B2	**B**	**Dry**	$274.72 \times 27.25^{\frac{1}{Spacing}}$	0.67	110.3	301.1
		Wet	$808.1 \div (1 - 79.3 * e^{-0.15 * Spacing})$	0.58	230.9	349.5
		Total	$1,127.5 \div (1 - 87.5 * e^{-0.16 * Spacing})$	0.69	289.5	364.0
	T	**Dry**	–	–	–	–
		Wet	$306.2 \div (1 - 98.4 * e^{-0.16 * Spacing})$	0.52	145.1	319.8
		Total	$519.9 \div (1 - 83.8 * e^{-0.149 * Spacing})$	0.49	200.3	340.4
	WUE	**Dry**	–	–	–	–
		Wet	–	–	–	–
		Total	–	–	–	–
C3	**B**	**Dry**	–	–	–	–
		Wet	–	–	–	–
		Total	–	–	–	–
	T	**Dry**	–	–	–	–
		Wet	$594.4 - 82.3 \times ln(spacing)$	0.21	94.3	291.0
		Total	$810.8 - 10.13 \times spacing$	0.11	148.4	320.0
	WUE	**Dry**	–	–	–	–
		Wet	$1.49 + 0.0477 \times spacing$	0.34	0.34	−68.5
		Total	–	–	–	–
IP	**B**	**Dry**	$275.28 \times 13.02^{\frac{1}{Spacing}}$	0.33	145.0	319.0
		Wet	$759.93 \times 6.87^{\frac{1}{Spacing}}$	0.25	323.3	369.9
		Total	$1,028.5 \times 8.32^{\frac{1}{Spacing}}$	0.29	460.8	392.0
	T	**Dry**	–	–	–	–
		Wet				
		Total				
	WUE	**Dry**	–	–	–	–
		Wet	–	–	–	–
		Total	–	–	–	–

E: Standard Error. AIC: Akaike Information Criterion. For all equations, degree of freedom = 30.

Araujo),Comigo (Ubirajara Oliveira), Copener (Jacyr Alves), Duratex (Raul Chaves), Eldorado (Vinicius Silva), Fazenda Campo Bom (Jacqueline Pirez), Fibria (Rodolfo Loos), Florestal Itaquari (Admir Mora), Forestal Oriental (Ricardo Methol), Gerdau (Francisco Gomes), GMR (Paulo Leite), International Paper (Cristiane Lemos), Jari (Katia Silva), Klabin (James Stahl), Lwarcel (Marcela Capoani), Montes del Plata (Alejandro Gonzalez), Plantar (David Fernandes), Rigesa (Ricardo Paim), Suzano (Luiz Fabiano and Leandro de Siqueira), Vallourec (Helder Andrade, in memoriam) and Veracel (Helton Lourenço). Several universities and institutes also supported TECHS: University of Sao Paulo, Sao Paulo State University, Federal University of Lavras, Federal University of Rio Grande do Norte, Colorado State University,

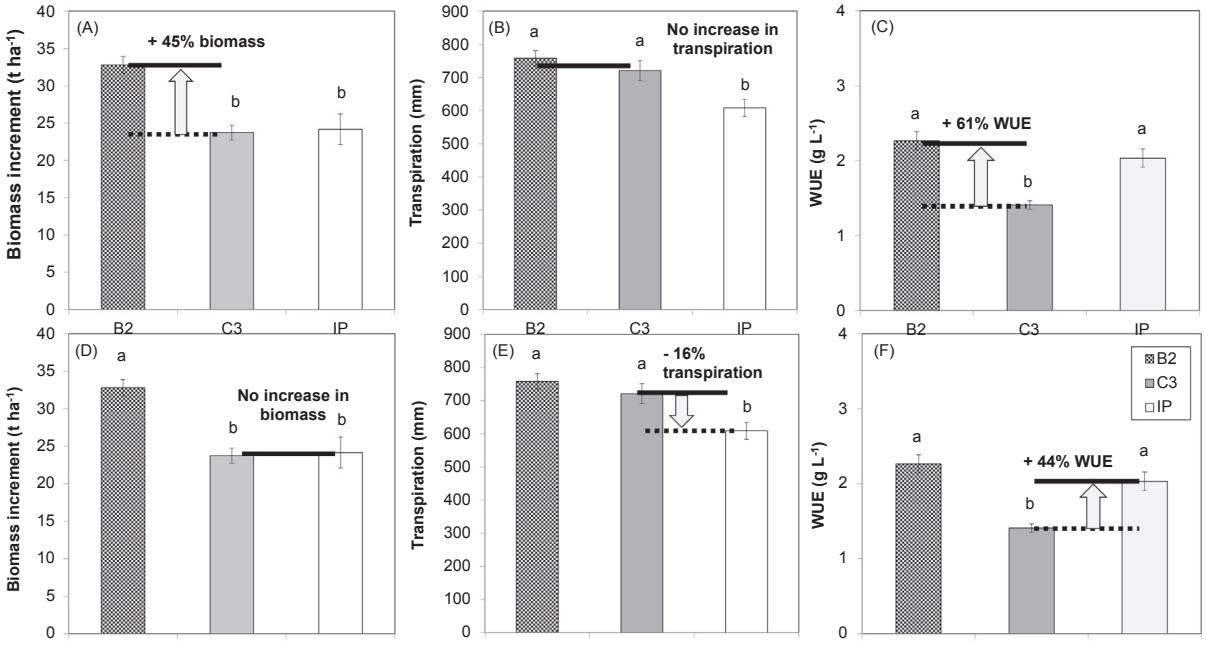

Fig. 6. Biomass increment, transpiration, and water use efficiency (WUE) at a density of 1420 trees ha^{-1}, showing changes, relative to the clone C3, in the clones B2 (A, B, C) and IP (D, E, F). Error bars represent standard error of the mean.

North Carolina State University, and the USDA Forest Service. This study was supported by a scholarship from CAPES (Coordination for the Improvement of Higher Education Personnel).

References

ABRAF – Brazilian Association of Forest Plantation Producers, 2013. ABRAF Statistical Year Book – Base Year 2012. Brasília 150.

Albaugh, J., Dye, P.J., King, K., 2013. Eucalyptus and water use in South Africa. Int. J. Forest Res. 2013, 1–11.

Almeida, A.C., Landsberg, J.J., Sands, P.J., 2004. Parametrization of 3-PG model for fast growing *Eucalyptus grandis* plantations. For. Ecol. Manage. 193, 179–195.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Goncalves, J.L.M., Sparovek, G., 2013. Koppen's climate classification map for Brazil. Meteorologische Zeitschrif 22, 1–18.

Battie-Laclau, P., Delgado-Rojas, J.S., Christina, M., Nouvellon, Y., Bouillet, J.P., de Cassia Piccolo, M., Laclau, J.P., 2016. Potassium fertilization increases water-use efficiency for stem biomass production without affecting intrinsic water-use efficiency in *Eucalyptus grandis* plantations. For. Ecol. Manage. 364, 77–89.

Binkley, D., Campoe, O.C., Alvares, C.A., Carneiro, R.L., Stape, J.L., 2020. Variation in whole-rotation yield among *Eucalyptus* genotypes in response to water and heat stresses: The TECHS project. Forest Ecol. Manag. https://doi.org/10.1016/j.foreco.2020.117953. (this issue).

Binkley, D., Campoe, O.C., Alvares, C., Carneiro, R.L., Cegatta, I., Stape, J.L., 2017. The interactions of climate, spacing and genetics on clonal Eucalyptus plantations across Brazil and Uruguay. For. Ecol. Manage. 405, 271–283.

Booth, T.H., 2013. Eucalypt plantations and climate change. For. Ecol. Manage. 301, 28–34.

Breda, N., 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. J. Exp. Bot. 54, 2403–2417.

Campoe, O.C., 2020. Patterns in carbon allocation among Eucalyptus clones across sites in Brazil. For. Ecol. Manage (in preparation).

Christina, M., le Maire, G., Nouvellon, Y., Vezy, R., Bordon, B., Battie-Laclau, P., Goncalves, 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. 148, 4–14.

Demattê. 2000. Levantamento semi-detalhado dos solos da Champion Papel e Celulose. Mogi Guaçu, Champion Papel e Celulose, 85 pp.

Eldridge, K., Davidson, J., Harwood, C., van Wyk, G., 1993. Eucalypt Domestication and Breeding. Clarendon Press, Oxford, pp. 60–72.

Falkenmark, M., Rockström, J., 2006. The new blue and green water paradigm: breaking new ground for water resources planning and management. J. Water Resour. Plann. Manage. 132, 129–132.

Ferraz, S.F.B., Lima, W.P., Rodrigues, C.B., 2013. Managing forest plantation landscapes for water conservation. For. Ecol. Manage. 301, 58–66.

Forrester, D.I., Collopy, J.J., Beadle, C.L., Warren, C.R., Baker, T.G., 2012. Effect of thinning, pruning and nitrogen fertilizer application on transpiration, photosynthesis and water use efficiency in a young *Eucalyptus nitens* plantation. For. Ecol. Manage. 266, 286–300.

Forrester, D.I., Wiedemann, J.C., Forrester, R.I., Baker, T.G., 2013. Effects of planting density and site quality on mean tree size and total stand growth of Eucalyptus globulus plantations. Can. J. For. Res. 43, 846–851.

Gonçalves, J.L.M., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., Ferraz, S.F.B., Lima, W.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. Manage. 301, 6–27.

Gonçalves, J.L.M., Stape, J.L., Laclau, J.P., Bouillet, J.P., Ranger, J., 2008. Assessing the effects of early silvicultural management on long-term site productivity of fast-growing eucalypt plantations: the Brazilian experience. Southern Forests 70, 105–118.

Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3, 309–320.

Grime, V.L., Sinclair, F.L., 1999. Sources of error in stem heat balance sap flow measurements. Agric. For. Meteorol. 94 (2), 103–121.

Hamer, J.J., Veneklaas, E.J., Renton, M., Poot, P., 2016. Links between soil texture and root architecture of Eucalyptus species may limit distribution ranges under future climates. Plant Soil 403, 217–229.

Hubbard, R.M., Stape, J.L., Ryan, M.G., Almeida, A.C., Rojas, J., 2010. Effects of irrigation on water use and water use efficiency in two fast growing *Eucalyptus* plantations. For. Ecol. Manage. 259, 1714–1721.

INDUFOR, 2012. Strategic Review on the Future of Forest Plantations in the World.. Study done for the Forest Stewardship Council (FSC), Bonn, Germany, pp. 1–11.

Kallarackal, J., Somen, C.K., 1997. Water use by *Eucalyptus tereticornis* stands of differing density in southern India. Tree Physiol. 17, 195–203.

Laclau, J.P., Silva, E.A.D., Rodrigues Lambais, G., Bernoux, M., Le Maire, G., Stape, J.L., Bouillet, J.P., Jourdan, C., Gonçalves, J.L.M., Nouvellon, Y., 2013. Dynamics of soil exploration by fine roots down to a depth of 10 m throughout the entire rotation in *Eucalyptus grandis* plantations. Front. Plant Sci. 4, 243.

Landsberg, J.J., Waring, R.H., 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95, 209–228.

Lesch, W., Scott, D.F., 1997. The response in water yield to the thinning of *Pinus radiata, Pinus patula* and *Eucalyptus grandis* plantations. For. Ecol. Manage. 99, 295–307.

Li, C., 2000. Population differences in water-use efficiency of *Eucalyptus microtheca* seedlings under different watering regimes. Physiol. Plant. 108, 134–139.

de Mattos, E.M., Binkley, D., Campoe, O.C., Alvares, C.A., Stape, J.L., 2020. Variation in canopy structure, leaf area, light interception and light use efficiency among *Eucalyptus* clones. For. Ecol. Manage. 463, 118038.

Myers, B.J., Theiveyanathan, S., O'Brien, N.D., Bond, W.J., 1996. Growth and water use of *Eucalyptus grandis* and *Pinus radiata* plantations irrigated with efluente. Tree Physiol. 16, 211–219.

Nelder, J.A., 1962. New kinds of systematic designs for spacing experiments. Biometrics 18, 283–307.

Nogueira, R., 2014. Caracterização anatômica foliar de 16 genótipos de Eucalyptus de alta produtividade do brasil. Dissertation, University of São Paulo State, Brazil, 103p.

Oda, M., Barbin, D., Stape, J.L., 2008. Aplicação de métodos geoestatísticos para identificação de dependência espacial na análise de dados de um ensaio de espaçamento florestal em delineamento sistemático tipo leque. Revista Árvore 32, 499–509.

Otto, M.S.G., Francisco, J.G., Gonsalez, B.T., de Almeida Calvo, L., de Mattos, E.M., de Almeida, M., de Andrade Moral, R., Demétrio, C.G.B., Stape, J.L., de Oliveira, R.F., 2017. Changes in γ-aminobutyric acid concentration, gas exchange, and leaf anatomy in *Eucalyptus* clones under drought stress and rewatering. Acta Physiol. Plant. 39, 208.

Otto, M.S.G., Hubbard, R., Binkley, D., Stape, J.L., 2014. Dominant clonal *Eucalyptus grandis* × *urophylla* trees use water more efficiently. For. Ecol. Manage. 328, 117–121.

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. Forest Ecol. Manage., 366, 143–152.

Reis, G.G.D., Reis, M.D.G.F., Fontan, I.D.C.I., Monte, M.A., Gomes, A.N., Oliveira, C.H.R.D., 2006. Crescimento de raízes e da parte aérea de clones de híbridos de *Eucalyptus grandis* x *Eucalyptus urophylla* e de *Eucalyptus camaldulensis x Eucalyptus* spp submetidos a dois regimes de irrigação no campo. Revista Árvore 30, 921–931.

Ryan, M.G., Stape, J.L., Binkley, D., Fonseca, S., Loos, R., Takahashi, E.N., Silva, C.R., Silva, S., Hakamada, R., Ferreira, J.M.A., 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 resource availability and stand structure alter production and carbon allocation. For. Ecol. Manage. 259, 1695–1703.

Schönau, A.P.G., Coetzee, J., 1989. Initial spacing, stand density and thinning in eucalypt plantations. For. Ecol. Manage. 29, 245–266.

Stape, J.L., Binkley, D., 2010. Insights from full-rotation Nelder spacing trials with *Eucalyptus* in São Paulo, Brazil. Southern For. 72, 91–98.

Stape, J.L., Binkley, D., Ryan, M.G., 2004. *Eucalyptus* production and the supply, use and the efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. For. Ecol. Manage. 193, 17–31.

Stape, J.L., Binkley, D., Ryan, M.G., Fonseca, S., Loos, R., Takahashi, E.N., Silva, C.R., Silva, S., Hakamada, R.E., Ferreira, J.M., Lima, A.M., Gava, J.L., Leite, F.P., Silva, G., Andrade, H., Alves, J.M., 2010. The Brazil *Eucalyptus* potential productivity project: influence of water, nutrients and stand uniformity on wood production. For. Ecol. Manage. 259, 1686–1694.

Stoneman, G.L., Crombie, D.S., Whitford, K., Hingston, F.J., Giles, R., Portlock, C.C., Galbraith, J.H., Dimmock, G.M., 1996. Growth and water relations of *Eucalyptus marginata* (jarrah) stands in response to thinning and fertilization. Tree Physiol. 17, 267–274.

Systat Software Inc., 2008. SigmaPlot for Windows. Version 10.0.

Vanclay, J.K., 2009. Managing water use from forest plantations. For. Ecol. Manage. 257, 385–389.

White, D.A., Crombie, D.S., Kinal, J., Battaglia, M., Mcgrath, J.F., Mendham, D., Walker, S.N., 2009. Managing productivity and drought risk in *Eucalyptus globulus* plantations in South-Western Australia. For. Ecol. Manage. 259, 33–44.

White, D.A., McGrath, J.F., Ryan, M.G., Battaglia, M., Mendham, D.S., Kinal, J., Downes, G.M., Crombie, D.S., Hunt, M.E., 2014. Managing for water-use efficient wood production in *Eucalyptus globulus* plantations. For. Ecol. Manage. 331, 272–280.

Whitehead, D., Beadle, C.L., 2004. Physiological regulation of productivity and water use in *Eucalyptus*: a review. For. Ecol. Manage. 193, 113–140.

Whitehead, D., Jarvis, P.G., Waring, R.H., 1984. Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. Can. J. For. Res. 14, 692–700.

Zobel, B.J., Wyk, G.V., Stahl, P., 1987. Growing exotic forests. John Wiley & Sons.