Biomass production and potential water stress increase with planting density in four highly productive clonal *Eucalyptus* genotypes[§]

Rodrigo Hakamada[1]*, Robert M Hubbard[2], Silvio Ferraz[3], José Luiz Stape[4] and Cristiane Lemos[5]

[1] *Forest Resources Graduate Program, 'Luiz de Queiroz' College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil*

[2] *US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA*

[3] *Forest Sciences Department, 'Luiz de Queiroz' College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil*

[4] *Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina, USA*

[5] *International Paper do Brasil, Mogi Guaçu, São Paulo, Brazil*

* Corresponding author, email: rodrigo_hakamada@yahoo.com.br

The choice of planting density and tree genotype are basic decisions when establishing a forest stand. Understanding the interaction between planting density and genotype, and their relationship with biomass production and potential water stress, is crucial as forest managers are faced with a changing climate. However, few studies have investigated this relationship, especially in areas with highly productive forests. This study aimed to determine the interaction between biomass production and leaf water potential, as a surrogate of potential water stress, in different clonal *Eucalyptus* genotypes across a range of planting densities. Four clones (two clones of *E. urophylla* × *E. grandis*, one clone of *E. urophylla*, and one clone of *E. grandis* × *E. camaldulensis*) and four planting densities (ranging from 591 to 2 949 trees ha⁻¹) were evaluated in an experimental stand in south-eastern Brazil. Biomass production was estimated 2.5 years after planting and predawn (ψ_{pd}) and midday (ψ_{md}) leaf water potential were measured 2 and 2.5 years after planting, in February (wet season) and August (dry season) in 2014. For all clones, total stand stemwood biomass production increased and leaf water potential decreased with planting density, and their interaction was significant. Thus, wood biomass at tighter spacings was higher but exhibited lower leaf water potentials, resulting in a trade-off between productivity and potential water stress. These are preliminary findings and still need to be supported by more experimental evidence and repetitions. However, in light of the increased frequency of extreme climate events, silvicultural practices that are tailored to the potential productivity of each region and that result in low potential water stress should be considered.

Keywords: Brazil, leaf water potential, plantation, wood productivity

Introduction

Global demand for wood products could triple by 2050 (WWF 2012). The reduction of natural forests, which are the main source of these resources, and the growing pressure for the conservation of these ecosystems underscore the importance of planted forests, which could supply up to 50% of the global demand for wood by 2050 (WWF 2012).

Planted forests, especially those established with trees of the *Eucalyptus* genus, comprise a relatively large share of the world economy. In Brazil, *Eucalyptus* plantations supply 35% of the current demand for wood, despite taking up only 1% of the land area, and contribute approximately 4% of gross domestic product and 20% of exports (ABRAF 2013).

The high productivity of *Eucalyptus* is the main aspect associated with its competitiveness (Stape et al. 2010). This high productivity is a result of the adaptation of the genus to different climate conditions, significant advances in breeding technology, and improvement of silvicultural practices (Gonçalves et al. 2017).

The choice of planting density is one of the critical steps in the process of planning and implementing plantation forest operations. The choice of planting density among trees is based on several factors, including the site productivity, rotation length, management system and costs, susceptibility of trees to water stress, and the use and final value of timber (Nyland 2002).

The first planting density experiment with *Eucalyptus* in Brazil was conducted by Andrade (1961), who found that maximum profitability and wood growth grown as a pulpwood or energy regime were achieved at planting densities between 1 000 and 1 500 trees ha⁻¹. Subsequently, several planting density trials have been planted in Brazil and around the world. These studies have focused on a number of issues, which include the effects of planting density on timber production (Balloni and Simões 1980; Schönau and Coetzee 1989; Bernardo et al. 1998; Neilsen and Gerrand 1999), branch size and development

(Alcorn et al. 2007; Forrester et al. 2013), nutrition (Harrison et al. 2000), and light-use efficiency (Silva 2006; Stape and Binkley 2010).

However, substantial gaps in knowledge of the interaction between plant genotypes and planting density remain as a result of recent trends, such as: (1) increased frequency of extreme climate events (Allen et al. 2010; Booth 2013), exposing plantations to elevated stress levels, especially water stress; (2) increased demand for planted forests in areas under high water stress (FAO 2013), particularly in northern and north-eastern Brazil; (3) the emergence of new pests and diseases, which may interact strongly with water stress and affect plant survival (Gonçalves et al. 2013); (4) the need for adaptation of silvicultural practices that reduce water use by planted forests in light of increased pressure for adoption of more sustainable practices (Ferraz et al. 2013); and (5) the use of highly productive genotypes, which may affect the genotype × planting density interaction (Forrester et al. 2013).

Experiments that investigate the interaction between genotypes, planting density and plant water stress are crucial to gain insights into these knowledge gaps. Bouvet (1997) conducted a large study evaluating the interaction between 40 eucalypt genotypes and three densities (625, 1 111 and 2 500 trees ha⁻¹). The results showed that at a juvenile age there was a significant interaction between genotype and spacing. Forrester et al. (2013) showed that for *Eucalyptus globulus* planted in contrasting climatic sites in Australia, the same trends of wood growth with changing spacing was observed in all sites. Thus, in this case, spacing does not interact with site quality for this species.

The present study aimed to determine the interaction between biomass production and leaf water potential (as a surrogate for potential water stress by Scholander et al. 1965) in different clonal *Eucalyptus* genotypes across a range of planting densities. We tested the hypothesis that higher total stand stemwood biomass production, regardless of tree genotype and stocking, are subjected to lower leaf water potential, resulting in a trade-off between plant productivity and potential water stress.

Materials and methods

Site description
The field experiment was set up in February 2014 in Mogi Guaçu, state of São Paulo, Brazil (22°20′58″ S, 46°58′16″ W; 664 m above sea level). The experiment is part of the Clonal Eucalyptus Tolerance to Water and Thermal Stress network (TECHS; http://www.ipef.br/techs/), which is an international collaborative research project involving 42 institutions (companies, universities and research centres) coordinated by the Brazilian Forestry Science and Research Institute (IPEF). The local climate is humid mesothermal (Cwa) according to the Köppen classification, with an average annual temperature of 22 °C and average annual precipitation of 1 200 mm, 81% of which is concentrated in summer (October to March). Water deficit in the region is 50 mm according to the Thornthwaite and Mather water balance model (Thornthwaite and Mather 1955), based on a 150 mm soil water storage capacity (Demattê 2000). Precipitation for the 2.5-year duration of

the study was 2 643 mm, 18% below the historical average, whereas the accumulated water deficit for the period was 279 mm, 109% greater than the historical average.

The stand where the experiment was established has been cultivated with eucalypts for over 50 years and at the end of the previous rotation (age 7) had a mean annual increment of 55 m³ ha⁻¹ y⁻¹, which is a high-productivity value for *Eucalyptus* plantations on a worldwide level (Gonçalves et al. 2013).

Experimental design
We used a systematic design with continuous and sequential increases in tree spacing (Figure 1). This design is effective to evaluate different genotypes across a wide range of planting densities in a small area (Stape and Binkley 2010). In this study, plots contained 14 trees (eight trees per measurement plot). Between-row spacing was 3.0 m and within-planting-row spacing varied according to the desired planting density (1.1, 2.3, 3.2 and 5.6 m), resulting in spacings of 3.4, 7.0, 9.7 and 16.9 m² tree⁻¹ (planting densities of 2 949, 1 424, 1 028 and 591 trees ha⁻¹) (Figure 1). The selected range corresponds to planting densities used in the log sawmilling industry (591 trees ha⁻¹), pulpwood (1 000–1 500 trees ha⁻¹) and for the use of wood biomass for energy production (2 949 trees ha⁻¹) (Balloni and Simões 1980). Neighbouring trees are not spatially independent, but we think they provide a fair estimate of tree physiology because any interaction between trees is competitive, leading to increased (rather than decreased) variation in physiology, and also encompassing realistic competitive interactions that happen in operational plantations. Because of the lack of replication at the plot level, results presented here should be viewed as preliminary findings. Further studies and replications need to be done to support the tentative conclusions drawn from this paper.

Four clonal genotypes with different origins from different *Eucalyptus* species/hybrids were investigated (Table 1). In short, we evaluated four clones × eight trees per clone × four planting densities, totaling 128 trees. The four clones occupied a total area of 7 560 m². The site is very uniform, but slight differences in soils might have some influence on tree physiology. However, the four-fold range in spacing is likely a much stronger factor than any minor variation in soils.

Soil preparation consisted of subsoiling to 60 cm depth every 3 m of row spacing. Rates of fertilisation were tailored to remove nutritional limitations (Gonçalves et al. 2013). Fertiliser applications consisted of 70, 110, and 160 kg of N, P and K, respectively, applied at the planting date (all P, 33% of N and K) and six and 12 months after planting (33% of N and K in each operation). The study plots were kept completely free of pests and diseases, and weed competition was suppressed since planting. Survival rates were 100% at all planting densities for both experimental and buffer trees not affecting the regression analyses (Oda et al. 2008).

Tree growth measurements
Growth rates were determined from tree height (*H*) and diameter at breast height (DBH, 1.3 m above the soil surface) measured 2.5 years after planting in August 2014.
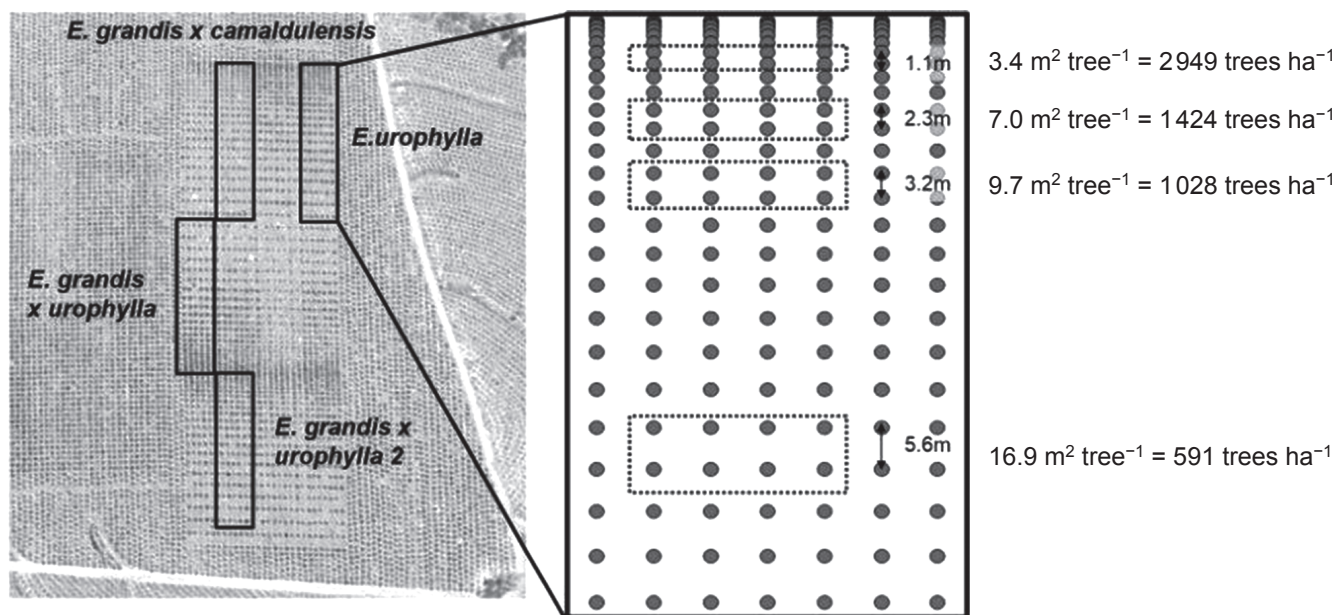
Figure 1: Satellite image of the study site showing the distribution of the four *Eucalyptus* clones (left) and graphical representation of plant spacing and corresponding planting densities (right). Dotted rectangles represent planting densities of 591, 1 028, 1 424 and 2 949 trees ha^{-1}. The Google Earth® image was captured 12 months after planting

Table 1: Species, clone, site of origin, climate characteristics for the sites, and water deficit for the four *Eucalyptus* clones evaluated in the study

Species	Clone	Origin (state)	Mean annual temperature (°C)	Mean annual rainfall (mm)[a]	Mean annual water deficit (mm)[a]
E. urophylla × *E. grandis*	Urograndis	Minas Gerais	22	1 200	0
E. urophylla	Urophylla	São Paulo	21	1 300	59
E. urophylla × *E. grandis* 2	Urograndis2	Minas Gerais	20	1 400	70
E. grandis × *E. camaldulensis*	Grancam	Bahia	24	1 450	165

[a] Source: Sentelhas et al. (1999)

Tree height and circumference at breast height (CBH) were measured using an electronic hypsometer and a tape measure, respectively. The CBH was later converted into DBH. Tree volume was estimated using DBH and *H* data in accordance with the model of Schumacher and Hall (1933) and converted into individual stemwood biomass by multiplying individual stemwood volume per basic density of each *Eucalyptus* clone. We harvested eight trees per clone in a nearby trial (<200 m) to determine wood density (R Hakamada unpublished data). Next, we used the individual stemwood tree as the unit of observation so that each of the eight tree-level biomass values was extrapolated to total stand stemwood biomass per hectare.

Measurements of leaf water potential

Leaf water potential (Ψ) measurements were conducted 2.0 and 2.5 years after planting in February and August 2014, representing the wet and dry seasons, respectively. Predawn Ψ (Ψ_{pd}) and midday Ψ (Ψ_{md}) measurements were taken between 03:00 and 06:00, and between 11:00 and 14:00, respectively, using a PMS1003 (PMS Instrument Co., Corvallis, OR, USA) Scholander-type pressure chamber (Scholander et al. 1965). Predawn measurements were used as a proxy for soil water potential and therefore soil water availability. Fully expanded and healthy leaves from the middle third of the canopy, chosen for Ψ_{pd} and Ψ_{md} measurements, were selected. We collected two leaves per tree from four trees per planting density, totalling eight leaves per planting density in the four clones evaluated (total per sample: 2 leaves × 4 trees × 4 planting densities × 4 clones = 128 leaves). The time between leaf excision and chamber pressurisation was <30 s.

Statistical analysis

Linear regression models were created using individual and total stand stemwood biomass and leaf water potential as independent variables and planting density as dependent variable (Figures 2 and 3). To compare the difference between genotypes, we used an identity test proposed by Leite and Oliveira (2006) that has been widely used to compare analytical methods in forestry. The unit of observation was the individual tree for this evaluation of tree physiology response to varying planting density. As a conservative measure, we also analysed the effect of planting density by pooling all eight trees at each spacing into a single average of biomass and Ψ, giving four

observations for testing the effect of planting density. The average trend would be the same in this analysis, but the reduction in degrees of freedom gives a far more conservative test of the effects of planting density than in our basic design that used each tree as a unit of observation.

Our design has 100% of survival across all plots, all neighbouring trees with similar size in all plots, and the site and soil properties were very uniform. That is why we provide an estimated total stand stemwood biomass per hectare for each treatment on a secondary y-axis, in addition to the primary y-axis that shows the biomass per tree, which, strictly speaking, was the basic unit of experimentation.

To compare whether the models of the two clones were different, we used a test of identity as proposed by Leite and Oliveira (2006). A logarithmic regression was used to determine the correlation between total stand stemwood biomass 2.5 years after planting (dependent variable) and leaf water potential (independent variable) (Figure 4). All analyses were performed using SAS/STAT® 9.3 software (SAS Institute 2011).

Results

Biomass production
Individual tree stemwood biomass decreased with increased planting density in the four *Eucalyptus* clones evaluated. Mean individual tree stemwood biomass was 52 kg tree^{-1} (range: 47–57 kg tree^{-1}) at a planting density of 591 trees ha^{-1} and 17 kg tree^{-1} (range: 13–24 kg tree^{-1}) at 2 949 trees ha^{-1} (Figure 2a). Conversely, total stand stemwood biomass (t ha^{-1}) increased with increased planting density for each clone. Total stand stemwood biomass accumulation at the highest stand density was 51 t ha^{-1} at 2.5 years after planting, 39% higher than at the lowest stand density (31 t ha^{-1}) (Figure 2b).

The response of total stand stemwood biomass to planting density differed among the clones. A 127% increase in total stand stemwood biomass was observed in the Urograndis clone from the lowest to the highest planting density, and increases of 52% and 49% were observed in the Urophylla and Urograndis2 clones, respectively. The Grancam clone showed the weakest response to planting density, with only a 34% increase in total stand stemwood biomass between the 591 and 2 949 trees ha^{-1} densities.

Leaf water potential in relation to planting density and genotypes
Leaf water potential was measured in the wet (February) and dry (August) seasons. Wet season predawn leaf water potential (Ψ_{pd}) was not significantly affected by planting density and did not vary across clones (mean = −0.25 MPa, range: −0.21 to −0.31 MPa; Figure 3a). However, all clones showed a trend towards Ψ_{md} reduction as planting density decreases (Figure 3b). Mean leaf Ψ_{md} was −1.7 MPa at a planting density of 2 949 trees ha^{-1} and −1.2 MPa at 591 trees ha^{-1}. In addition, mean leaf Ψ_{md} differed significantly across clones; the Grancam clone had the lowest mean Ψ_{md} (−2.1 MPa), followed by Urograndis2, Urophylla and Urograndis clones (−1,6, −1.1 and −0.9 MPa, respectively).

Dry season predawn and midday leaf Ψ were negatively affected by planting density and varied across clones. Mean Ψ_{pd} for all clones was −1.7 MPa at the highest planting density, 28% lower than at the lowest planting density (−1.2 MPa) (Figure 3c), whereas mean Ψ_{md} was −3.2 MPa at the highest planting density, 33% lower than at the lowest planting density (−2.2 MPa) (Figure 3d). The Urograndis clone had the lowest dry season leaf Ψ, followed by the Urophylla, Urograndis2 and Grancam clones.

Relationship between total stand stemwood biomass and leaf water potential
Dry season predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential correlated negatively with total stand stemwood biomass production 2.5 years after planting ($R^2 = 0.58$, $p < 0.001$; Figure 4). This result was independent of genetic material, i.e. the higher the total stand stemwood biomass in each treatment, the lower the leaf water potential.
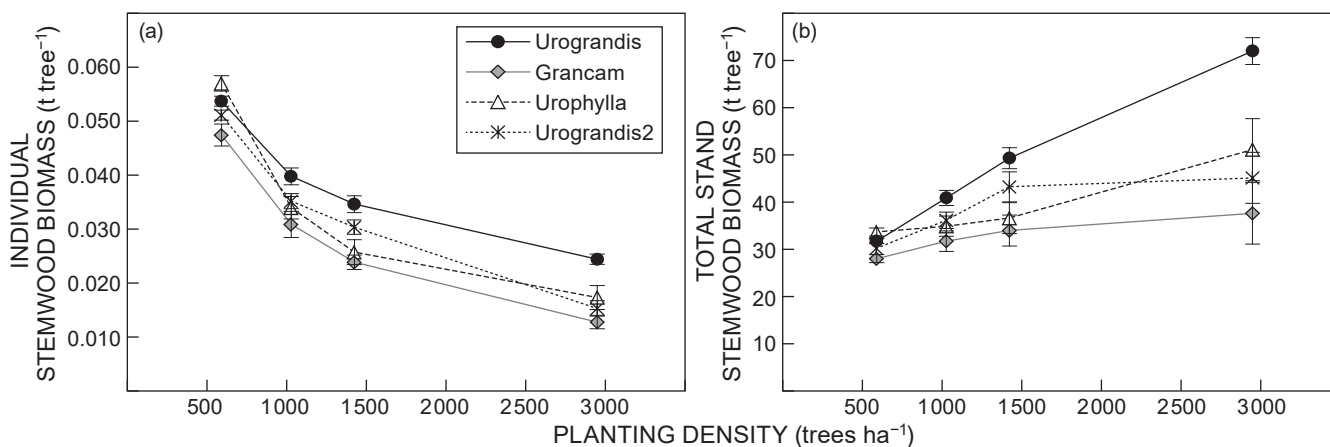

Figure 2: Relationship between individual (a) and total stand (b) stemwood biomass per clone in relation to planting density (trees ha^{-1}). Error bars represent the standard error among trees ($n = 8$). All clones had the logarithmic regression adjusted between planting density and individual ($p < 0.01$, $R^2 > 0.79$) and total stand stemwood biomass ($p < 0.01$, $R^2 > 0.22$). Genotypes regressions were compared using identity test

Discussion

In our study, we showed that biomass production and leaf water potential were affected by planting density and tree genotype; total stand stemwood biomass increased with planting density regardless of genotype. This result follows the typical pattern of spacing experiments with various genera such as *Eucalyptus* (Stape and Binkley 2010; Forrester et al. 2013), *Pinus* (Blevins et al. 2005), and *Populus* (Toillon et al. 2013). However, in our study, biomass production rates varied among genotypes. Clones of species with high leaf area index (LAI), i.e. *E. urophylla* (Xavier et al. 2002), showed a greater increase in productivity with increasing planting density. Conversely, the
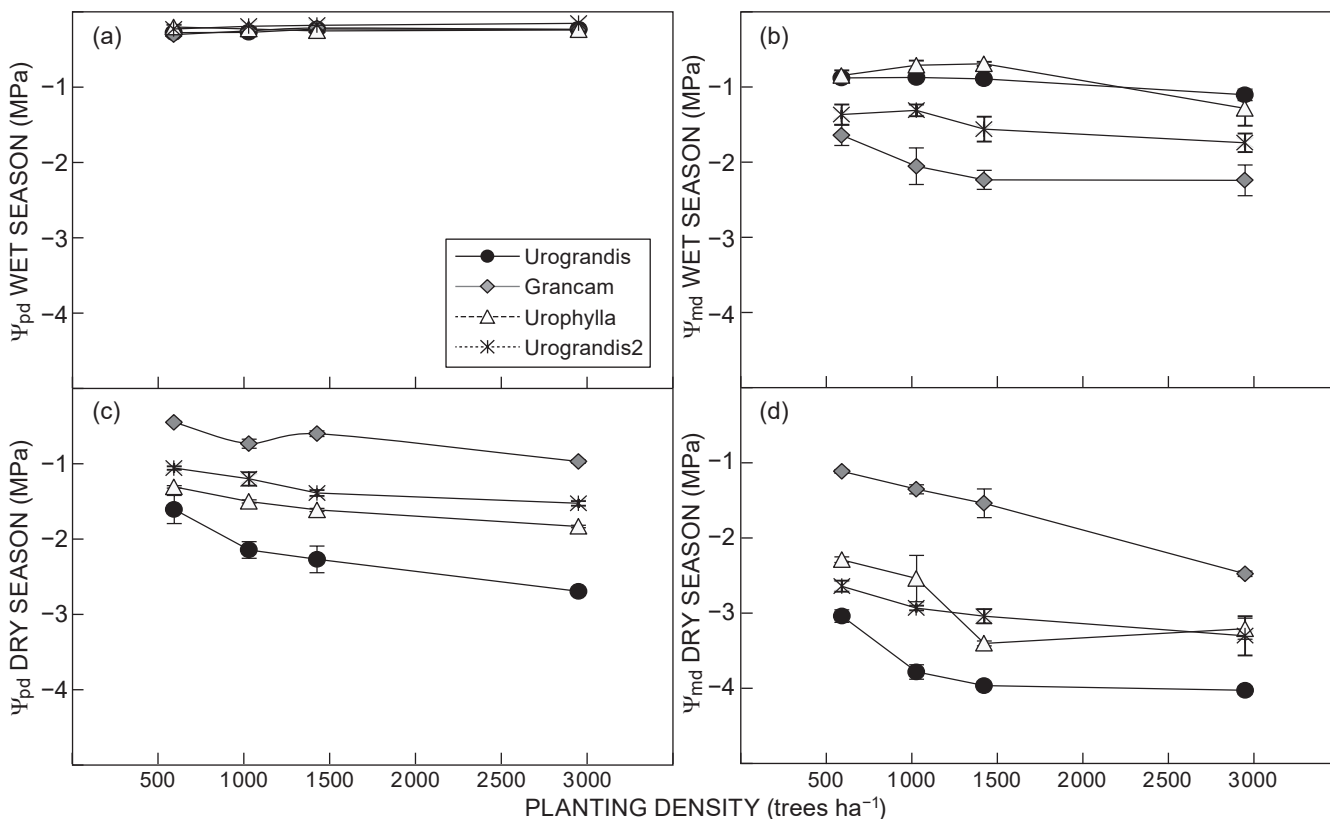
Figure 3: Relationship between predawn (Ψ_{pd}) (a and c) and midday (Ψ_{md}) (b and d) leaf water potential and planting density (trees ha^{-1}) in wet (February) and dry (August) season. Bars represent the standard error among trees ($n = 8$). With the exception of Ψ_{pd} in the wet season (non-significant), all clones had the logarithmic regression adjusted between planting density and Ψ_{md} in the wet season ($p < 0.05$, $R^2 > 0.15$), Ψ_{pd} in the dry season ($p < 0.01$, $R^2 > 0.51$) and Ψ_{md} in the dry season ($p < 0.01$, $R^2 > 0.33$)
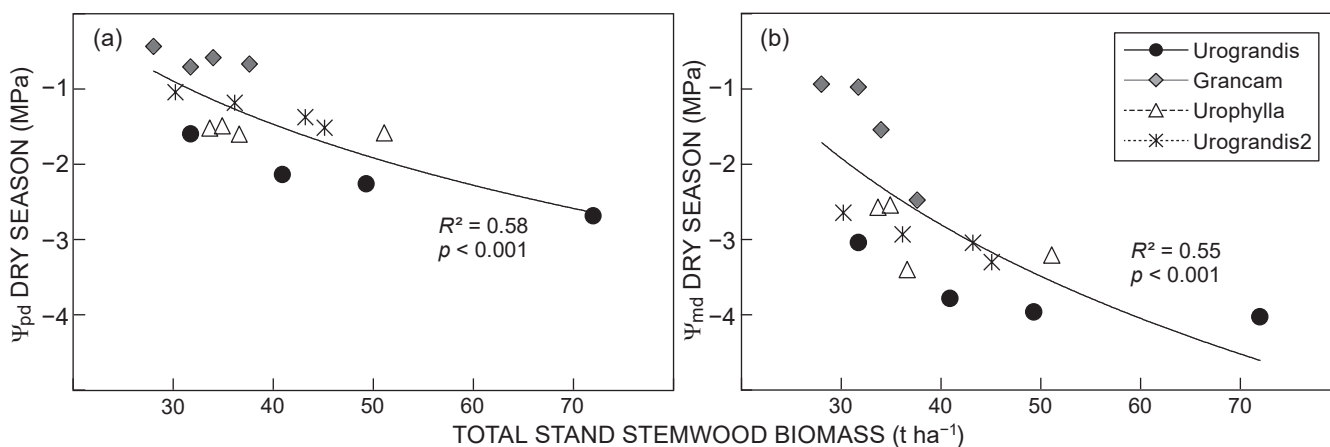
Figure 4: Relation between dry season (August) predawn (Ψ_{pd}) (a) and midday (Ψ_{md}) (b) leaf water potential with cumulative total stand stemwood biomass (t ha^{-1}) 2.5 years after planting

Grancam clone, which is a hybrid of *E. camaldulensis* (James and Bell 1995) and has a low LAI, showed a small increase in productivity with increasing planting density.

Clones with the greatest increase in total stand stemwood biomass also had the lowest leaf Ψ_{pd} and Ψ_{md}. Interestingly, Ψ values followed the inverse of the water deficit of the region that the clones were selected for under field conditions (Table 1). The hybrid of *E. camaldulensis* and *E. grandis*, which was selected in a high water deficit region, had the highest least negative Ψ_{pd} and Ψ_{md} readings. Conversely, Urograndis, which was selected in an area with minimal water deficits, had the lowest most negative Ψ value in the dry season. The lowest Ψ_{md} observed in an individual measurement was −4.2 MPa for an Urograndis sample, which is an extremely low value for *Eucalyptus* (Whitehead and Beadle 2004). According to Arndt et al. (2014), rainfall at the site of origin in the natural habitat of the different *Eucalyptus* species has a direct effect on traits related to water stress tolerance, such as turgor loss point, a trait that has been used to try to identify the tolerance level of species to drought (Bartlett et al. 2014). Thus, the higher the rainfall at the site of origin, the lower the drought tolerance. Given that water supply is a key resource determining levels of plantation productivity (Stape et al. 2010), the study of Arndt et al. (2014) is consistent with the findings of our study, indicating that high-yielding genotypes are likely to deplete water resources faster than low-yielding genotypes, and therefore are more likely to suffer from drought.

Kallarackal and Somen (1997) investigated the effect of planting density on leaf water potential in *Eucalyptus tereticornis* and found that leaf Ψ_{pd} was twice as high at a stocking of ≈1 000 trees ha−1 than at 1 800 trees ha−1. Other studies regarding different species also detected a reduction in leaf Ψ with increasing stocking, as in *Eucalyptus globulus* (Donoso and Ruiz 2001; White et al. 2009), Douglas-fir (Aussenac and Granier 1988), *Pinus contorta* (Donner and Running 1986) and *Quercus petraea* (Bréda et al. 1995). However, in these previous studies, productivity was not greater than 30 m³ ha−1 y−1. To our knowledge, this is the first study on the relationship between leaf water potential and timber production in high-productivity *Eucalyptus* stands. Our results show that highly productive stands are associated with an increased risk of water stress, especially in light of the current scenario of extreme climate events. Thus, we propose that forest managers should not follow silvicultural practices (genotypes + planting density) aimed at achieving maximum productivity in areas prone to drought. Ideally, silvicultural practices should be tailored to the potential productivity of each region and tree spacing optimised to achieve timber production goals while minimising potential water stress.

In order to maximise carbon gain in the face of the near-constant trade-off between photosynthesis and water loss via transpiration, many woody plant species regulate stomatal conductance to maintain leaf and plant water potential near the point of catastrophic xylem failure (Tyree and Sperry 1988). Consequently, although leaf water potential can be a good indicator of plant water status (Scholander et al. 1965) low leaf water potential is not necessarily a precursor to tree mortality (McDowell et al. 2008).

An experiment at one site over the course of a single year does not provide statistically based insights into other years and locations. However, the patterns of growth and leaf water potential in relation to planting density were so clear that we expect trees in other years and locations would show similar trends.

The current study is located in a medium water deficit region (Alvares et al. 2013). However, we would expect that in lower water availability regions potential water stress increment will be higher with total stand stemwood biomass productivity increase, and the opposite would be true in areas with higher water availability. Further studies aimed at identifying specific drought tolerance mechanisms and strategies of *Eucalyptus* clones and genotypes carried out at different water availability regions are needed so that silvicultural planning can be optimised for specific conditions in face of more frequent and prolonged drought periods.

References

ABRAF (Brazilian Association of Forest Plantation Producers). 2013. *ABRAF statistical yearbook 2013 – base year 2012*. Brasília: ABRAF.

Alcorn PJ, Pyttel P, Bauhus J, Smith RGB, Thomas D, James R, Nicotra A. 2007. Effects of initial planting density on branch development in 4-year-old plantation grown *Eucalyptus pilularis* and *Eucalyptus cloeziana* trees. *Forest Ecology and Management* 252: 41–51.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660–684.

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728.

Andrade EN. 1961. *O eucalipto* (2nd edn). Jundiai: CPEF.

Arndt S, Sanders G, Hirsch M. 2014. Hydraulic and ecophysiological traits related to tree drought mortality are linked to the aridity of the environment in eucalypts. In: Parrotta JA, Moser CF, Scherzer AJ, Koerth NF, Lederle DR (eds), Sustaining forests, sustaining people: the role of research [XXIV IUFRO World Congress, 5–11 October 2014, Salt Lake City, USA – Abstracts]. *International Forestry Review* 16(5): 236.

Aussenac G, Granier A. 1988. Effects of thinning on water stress and growth in Douglas-fir. *Canadian Journal of Forest Research* 18: 100–105.

Balloni EA, Simões JW. 1980. O espaçamento de plantio e suas implicações silviculturais. *IPEF – Série Técnica* 1(3): 1–16.

Bartlett MK, Zhang Y, Kreidler N, Sun S, Ardy R, Cao K, Sack L. 2014. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters* 17: 1580–1590.

Bernardo AL, Reis MGF, Reis GG, Harrison RB, Firme DJ. 1998. Effect of spacing on growth and biomass distribution in

Eucalyptus camaldulensis, *E. pellita* and *E. urophylla* plantations in southeastern Brazil. *Forest Ecology and Management* 104: 1–13.

Blevins DP, Prescott CE, Allen HL, Newsome TA. 2005. The effects of nutrition and density on growth, foliage biomass, and growth efficiency of high-density fire-origin lodgepole pine in central British Columbia. *Canadian Journal of Forest Research* 35: 2851–2859.

Booth TH. 2013. *Eucalyptus* and climate change. *Forest Ecology and Management* 301: 28–34.

Bouvet JM. 1997. Effect of spacing on juvenile growth and variability of *Eucalyptus* clones. *Canadian Journal of Forest Research* 27: 174–179.

Bréda N, Granier A, Aussenac G. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology* 15: 295–306.

Demattê A. 2000. Levantamento semi-detalhado dos solos da Champion Papel e Celulose. Mogi Guaçu: Champion Papel e Celulose.

Donner BL, Running SW. 1986. Water stress response after thinning *Pinus contorta* stands in Montana. *Forest Science* 32: 614–625.

Donoso S, Ruiz F. 2001. Potencial hídrico y crecimiento de *Eucalyptus globulus* plantado a diferentes espaciamientos en la Provincia de Huelva, España. *Bosque* 22: 37–44.

FAO (Food and Agriculture Organization of the United Nations). 2013. Summary report of the 3rd International Congress on Planted Forests. 2013. Rome: FAO.

Ferraz SFB, Lima WP, Rodrigues CB. 2013. Managing forest plantation landscapes for water conservation. *Forest Ecology and Management* 301: 58–66.

Forrester DI, Wiedemann JC, Forrester RI, Baker TG. 2013. Effects of planting density and site quality on mean tree size and total stand growth of *Eucalyptus globulus* plantations. *Canadian Journal of Forest Research* 43: 846–851.

Gonçalves JLM, Alvares CA, Higa AR, Silva LD, Alfenas AC, Stahl J, Ferraz SFB, Lima WP, Brancalion PHS, Hubner A, Bouillet J-PD, Laclau J-P, Nouvellon Y, Epron D. 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. *Forest Ecology and Management* 301: 6–27.

Gonçalves JLM, Alvares CA, Rocha JHT, Brandani CB, Hakamada RE. 2017. Eucalypt plantation management in regions with water stress. *Southern Forests*. DOI: 10.2989/20702620.2016.1255415.

Harrison RB, Reis GG, Reis MDGFA, Bernardo L, Firme DJ. 2000. Effect of spacing and age on nitrogen and phosphorus distribution in biomass of *Eucalyptus camaldulensis*, *Eucalyptus pellita* and *Eucalyptus urophylla* plantations in southeastern Brazil. *Forest Ecology and Management* 133: 167–177.

James SA, Bell DT. 1995. Morphology and anatomy of leaves of *Eucalyptus camaldulensis* clones: variation between geographically separated locations. *Australian Journal of Botany* 43: 415–433.

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

Leite HG, Oliveira FHT. 2006. Statistical procedure to test identity between analytical methods. *Communications in Soil Science and Plant Analysis* 33: 1105–1118.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Sperry J, West A, Williams D, Yepez EA. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.

Neilsen WA, Gerrand AM. 1999. Growth and branching habit of *Eucalyptus nitens* at different spacing and the effect of final crop selection. *Forest Ecology and Management* 123: 217–229.

Nyland RD. 2002. *Silviculture: concepts and applications*. Long Grove: Waveland Press.

Oda M, Barbin D, Stape JL. 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.

SAS Institute. 2011. *Base SAS® 9.3 procedures guide*. Cary: SAS Institute.

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA. 1965. Sap pressure in vascular plants. *Science* 143: 339–346.

Schönau APG, Coetzee J. 1989. Initial spacing, stand density and thinning in eucalypt plantations. *Forest Ecology and Management* 29: 245–266.

Schumacher FX, Hall FS. 1933. Logarithmic expression of timber-tree volume. *Journal of Agricultural Research* 7: 719–734.

Sentelhas PC, Pereira AR, Marin FR, Angelocci LR, Alfonsi RR, Caramori PH, Swart S. 1999. Balanços hídricos climatológicos do Brasil – 500 balanços hídricos de localidades brasileiras. Piracicaba: ESALQ [CD-ROM].

Silva CR. 2006. Efeito do espaçamento e do arranjo de plantio na produtividade e uniformidade de clones de *Eucalyptus* na região Nordeste do Estado de São Paulo. MSc thesis, University of São Paulo, Piracicaba, Brazil.

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

Stape JL, Binkley D, Ryan MG, Fonseca S, Loos R, Takahashi EN, Silva CR, Silva S, Hakamada R, Ferreira JM, Lima AM, Gava JL, Leite FP, Silva G, Andrade H, Alves JM. 2010. The Brazil Eucalyptus Potential Productivity Project: influence of water, nutrients and stand uniformity on wood production. *Forest Ecology and Management* 259: 1686–1694.

Thornthwaite CW, Mather JR. 1955. The water balance. *Publications in Climatology* 8(1): 1–86.

Toillon J, Fichot R, Dallé E, Berthelot A, Brignolas F, Marron N. 2013. Planting density affects growth and water-use efficiency depending on site in *Populus deltoides* × *P. nigra*. *Forest Ecology and Management* 304: 345–354.

Tyree MT, Sperry JS. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology* 88: 574–580.

White DA, Crombie DS, Kinal J, Battaglia M, Mcgrath JF, Mendham D, Walker SN. 2009. Managing productivity and drought risk in *Eucalyptus globulus* plantations in south-western Australia. *Forest Ecology and Management* 259: 33–44.

Whitehead D, Beadle CL. 2004. Physiological regulation of productivity and water use in *Eucalyptus*: a review. *Forest Ecology and Management* 193: 113–140.

WWF (World Wildlife Fund). 2012. *Living planet report 2012: biodiversity, biocapacity and better choices*. Gland: WWF.

Xavier AC, Soares JV, Almeida AC. 2002. Leaf area index changes with age among eucalypt clonal plantations. *Revista Árvore* 26: 421–427.