



Contrasting water use of two *Eucalyptus* clones across a precipitation and temperature gradient in Brazil

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ABSTRACT

Eucalyptus plantation productivity has increased 4-fold across Brazil as a result of improved genetic selection and intensive silviculture. However, the rate of productivity improvements is slowing and suggests increased production will require planting in areas that have never been previously planted with *Eucalyptus* with uncertain impacts on local water supplies. This study compares water use and water use efficiency between a drought resistant (*E. grandis* × *E. camaldulensis*) and high productivity *Eucalyptus* clone (*E. urophylla*) across three sites (dry, mesic and wet) spanning a two-fold precipitation gradient (~600–1350 mm y⁻¹) in Brazil. Each site included a 30% reduced rainfall treatment for each clone to investigate within site response to reduced precipitation. We found that the drought resistant clone used as much or more water than the high productivity clone at all three sites. The drought resistant clone transpired almost 20% percent more water than the high productivity clone at the dry site (3.7 vs. 3.0 m³ y⁻¹) while water use between clones did not differ at the mesic (4.6 vs 4.0 m³ y⁻¹) and wet site (4.0 vs 4.5 m³ y⁻¹). The high productivity clone transpired 54, 46 and 37% of annual precipitation at the dry, mesic and wet sites respectively while the drought resistant clone consumed 67, 47 and 31% of annual precipitation from the dry to the wet site. Although the rain reduction treatments did not impact annual water use for either clone at the dry and mesic sites, there were some differences at a subannual timescale. Rain reduction treatments at the dry site lowered transpiration in the driest, hottest three months for the high productivity clone by 25–32%. Rainfall reduction led to lower water use by the drought resistant clone for only one month during the dry season (18%). The high productivity clone transpired less water (24–26%) in the rainfall reduction treatment at the mesic site during three months and the drought resistant clone transpired 18 and 20% less water in the rainfall reduction treatment during two months. Rainfall reduction reduced annual transpiration by 59% for the high productivity clone at the wet site. Average water use efficiency of the drought resistant clone was almost 70% lower than the high productivity clone at the dry and mesic sites (~5.2 vs. 1.5 kg m⁻³ y⁻¹) and was due to the combination of low growth and high water use. Higher than expected growth by the drought resistant clone at the wet site resulted in similar water use efficiency between clones (6.3 vs. 5.8 kg m⁻³ y⁻¹). We discuss potential implications of our findings and highlight several lines of evidence that suggest the drought resistant clone in this study allocates a greater proportion of gross primary productivity below ground allowing it to access deeper reserves of soil water during dry periods. Our results suggest that decisions to plant drought resistant clones in drought prone areas should be carefully considered and also highlight the need for more research on water use and drought tolerance strategies for *Eucalyptus* clones bred for more arid areas in Brazil.

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Table 1
Tree and meteorological information for the high productivity (A1) and drought resistant (C3) clone at the three measurement sites. DBH = diameter at breast height, CAI = current annual increment, PAR = photosynthetically active radiation and VPD = air saturation deficit. Water deficit was calculated as the difference between potential and actual evapotranspiration.

Genotype	Dry – 30						Mesic-20						Wet – 22					
	Control			Exclusion 30%			Control			Exclusion 30%			Control			Exclusion 30%		
	A1	C3		A1	C3		A1	C3		A1	C3		A1	C3		A1	C3	
Mean DBH (cm ± se)	14.3 ± 0.3	11.9 ± 0.4		12.7 ± 41.0	11.8 ± 0.3		16.9 ± 0.6	14.9 ± 0.5		16.33 ± 0.5	14.4 ± 0.4		17.5 ± 0.5	18.9 ± 0.5		16.6 ± 0.5	18.9 ± 0.5	
DBH Max (cm)	15.6	14.2		15.1	13.1		21.0	17.6		19.2	16.4		19.8	21.0		18.9	21.0	
DBH Min (cm)	11.4	8.1		9.44	9.2		12.6	11.4		12.9	11.4		12.8	14.9		13.5	14.9	
CAI (kg ± se)	15.8 ± 1.4	6.3 ± 0.6		10.3 ± 1.2	5.4 ± 0.7		23.6 ± 3.7	6.3 ± 0.9		19.3 ± 2.5	7.4 ± 0.9		26.6 ± 3.9	27.0 ± 4.3		19.7 ± 3.3	27.0 ± 4.3	
Tree Spacing (m)	3 × 3																	
Temperature °C	24.7						21						18.05					
Min-Max	18.7–31.5						15.9–29.2						14.1–23.2					
Precipitation (mm)	622						1088						1380					
VPD (24 hr) (kPa)	1.6						1.0						0.5					
VPD (daylight) (kPa)	2.1						1.5						0.7					
RH %	55.42						69.3						79.4					
Min-Max	32.2–78.4						37.1–91.3						57.4–93.9					
PAR (μmol m ⁻² s ⁻¹)	983.3						835.2						854.2					
Water Deficit (mm)	698						100						2.5					

1. Introduction

Eucalyptus plantation productivity has increased 4-fold across Brazil as a result of improved genetic selection and intensive silviculture. However, the rate of increase in productivity is currently near zero (Binkley et al., 2017) suggesting that if forest companies are to increase wood production, they will need to plant additional hectares of plantations. Many companies are choosing to establish new plantations with drought resistant genotypes in areas that have never been previously planted with *Eucalyptus* and may be marginally suitable for *Eucalyptus* production. Tax incentives and government policies increase the economic opportunities on these marginal lands further favoring plantation establishment (Goncalves et al., 2013). New plantation establishment in areas that may be marginal for *Eucalyptus* provides a demand for drought resistant genotypes that survive, produce acceptable levels of growth, and minimize water use with low impacts on downstream communities.

Climate change will undoubtedly exacerbate existing conflicts between *Eucalyptus* forest industries and downstream water users as rising temperatures and changes in rainfall may also require drought resistant genotypes on land that is currently highly productive. Water stress will likely increase, as the Intergovernmental Panel on Climate Change predicts increases in surface air temperatures and decreases in rainfall for the tropics (Hoegh-Guldberg et al., 2018). Indeed, systematic rise in air saturation deficit (*D*) has already developed across much of South America (Barkhordarian et al., 2019). As climate change continues to impact both productivity and tree water use in *Eucalyptus* plantations, there is a growing need to understand the tradeoffs between wood production and water use for both drought resistant and high productivity *Eucalyptus* genotypes.

Water use by *Eucalyptus* plantations is a growing concern as many areas experience increased climate change impacts and population pressures necessitate careful regulation of water delivery to municipalities and agricultural interests. There are multiple studies and reviews highlighting the impact of plantation establishment on water delivery downstream (Bosch and Hewlett, 1982; Ferraz et al., 2019). In general, impacts of *Eucalyptus* plantations are greater in more arid locations (Albaugh et al., 2013) highlighting the need to understand the impacts of planting *Eucalyptus* in marginal areas.

Water use efficiency is the tradeoff between wood production and tree water use and is often used as a selection criteria within clonal *Eucalyptus* plantations (Dvorak, 2012). *Eucalyptus* WUE has been shown to increase with water availability (Stape et al., 2004) and has also been shown to increase with tree size (Otto et al., 2014). There is a large body of research describing how drought resistant and drought sensitive food crop cultivars differ in WUE during drought (Farooq et al., 2019; Ullah et al., 2019) but only a limited number of similar studies for forests. Because drought resistant clones are often selected for planting in dry areas (Dvorak, 2012) we need to understand how water use efficiency changes with resource availability for these clones and how they compare to other more productive and or less drought resistant genotypes.

The TECHS experimental platform (Binkley et al., 2017) enabled us to investigate tree water use and water use efficiency for a drought resistant and high productivity clone across a precipitation gradient of approximately 600–1350 mm and to quantify the impact of rainfall reduction treatments within each site. We tested three hypotheses:

- (1) The drought resistant clone would use less water compared to the high productivity clone at all three sites
- (2) Water use efficiency would be higher for the drought resistant versus the high productivity clone at each site and WUE would be lower in the rainfall reduction compared to control treatments.
- (3) The rainfall reduction treatment within each site would have less impact on tree water use for the drought resistant compared to the high productivity clone.

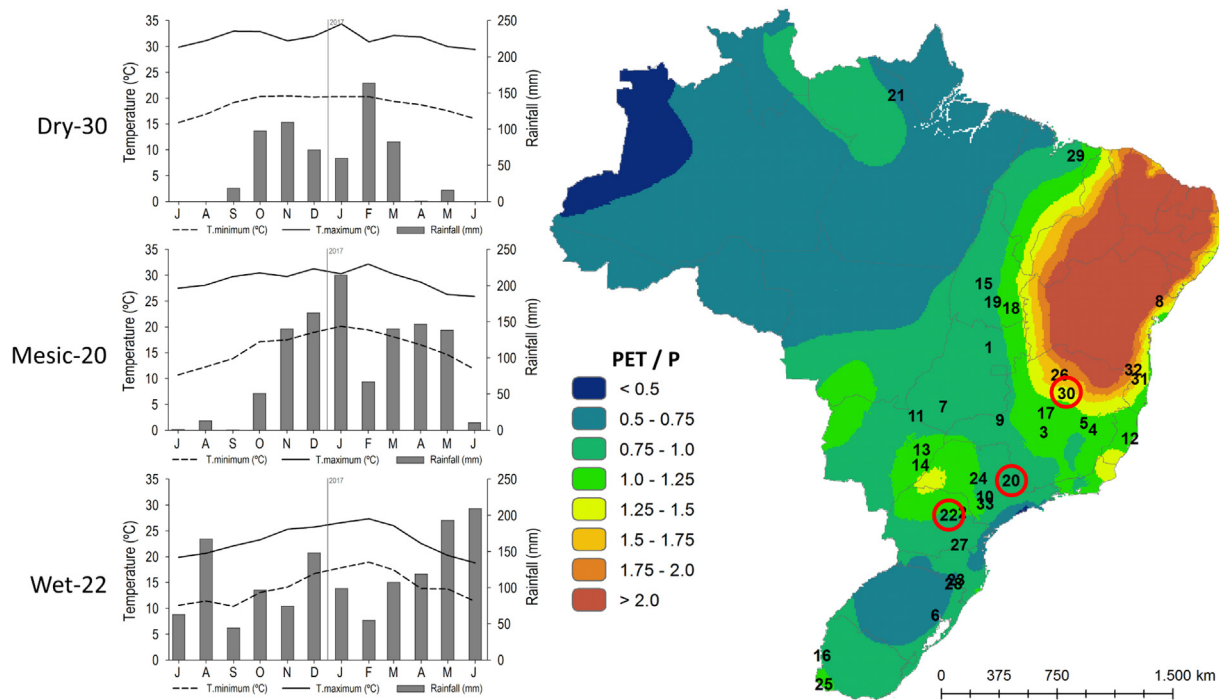


Fig. 1. Temperature and precipitation during the study period at each of the 3 research sites shown within the TECHS research platform across Brazil.

2. Methods

We chose three study sites within the TECHS experimental research platform (described in Binkley et al., 2017, 2020) that spanned a 2-fold range of annual precipitation and a 6-degree range in temperature. The driest, hottest site (#30) was located near Bocaiúva (17.32°S, 43.77°W), Brazil, with 622 mm y^{-1} of rain and an average annual temperature of 24.7 °C during our measurement period. The “mesic” site (#20) near the town of Mogi-Guaçu (24.23°S, 50.53°W), Brazil received 1088 mm y^{-1} of rain with a mean annual temperature of 21.0 °C and the wet site (#22) near the town of Telêmaco Borba (22.35 °C, 46.97°W), Brazil had 1380 mm y^{-1} of rain and average annual temperature was 18.05 °C. Water deficit (measured as the difference between Potential and Actual evapotranspiration) varied across our sites: 2.5, 100 and 698 mm yr^{-1} (Table 1).

The TECHS experimental design included four “plastic” clones that were planted at all 36 sites from the Tropics to the Subtropics (Fig. 1). We used two of these plastic clones that are commonly planted in contrasting environments (Fig. 2). The A1 clone (*E. urophylla*) is one of the most widely planted clones in Brazil, because of its high productivity across a wide range of sites (Caldeira et al., 2020). The C3 (*E. grandis* × *E. camaldulensis*) clone was developed in the state of Minas Gerais and is typically planted only in drier areas because lower growth rates are matched with higher resistance to drought. The clones were planted at a 3x3 meter spacing within a 0.2 ha plot at all three sites. Each plot was split to include a rainfall reduction treatment (~30% of canopy throughfall). Due to operational constraints, there was no rainfall reduction treatment for the C3 clone at the wet site. Measurements for this study began when trees were four years old. We obtained one year of continuous data (July 1, 2016 to June 30, 2017; plans for extending data collection were foiled by damage from lightning strikes and vandalism).

Meteorological data were collected at or near each site (< 1 km) using standard sensors connected to a data logger, including: air temperature, relative humidity, air saturation deficit (*D*), precipitation and total solar radiation at hourly intervals. We estimated photosynthetically active radiation (PAR) by regression analysis with global radiation using seven weather stations across tropical and subtropical

Brazil ($r^2 = 0.99$, $p < 0.0001$, data not shown).

Fifteen trees of each clone within the control and rainfall reduction plots were sampled, for a total of 60 trees at each site (180 trees across 3 sites). Trees selected for measurement represented the range of tree diameters on the plot. We installed thermal dissipation probes (Granier, 1985) to quantify tree transpiration following methods described in Hubbard et al. (2010). Briefly, a single 2-cm long sensor was installed in a randomly selected cardinal direction for each tree, approximately 10 cm above breast height. Sensors were moved every three months to account for the variation in sap velocity with circumference and to prevent over-growth of the probes. Probes were insulated with closed cell foam and covered with foil-backed insulation (Reflectix, Inc.) to prevent heating from solar radiation. Each probe was connected to a data logger equipped with a multiplexor (CR1000 and AM16/32, Campbell Scientific, Logan Utah) and temperature differences between the upper and lower needle were measured every minute and 15 min averages recorded. Sap velocity was calculated with a modified Granier equation that was calibrated for plantation grown *Eucalyptus* (Hubbard et al., 2010). Tree transpiration was estimated as the product of sap velocity and sapwood area (see below).

At the end of the study, we harvested nine of our measurement trees within the plots (all sites and treatments) and developed a relationship between tree diameter and sapwood area at the probe location. We used this relationship to quantify sapwood area and sapwood thickness for each tree, clone, treatment and site. When sapwood thickness was less than 2 cm, we adjusted sap velocity estimates using the equation proposed by Clearwater and Meinzer (2001). In some cases, sapwood thickness exceeded 2 cm but we lacked the proper sensors to quantify the radial profiles of sap flux density in these trees. Instead, we used the radial profile equation for diffuse porous species from Berdanier et al. (2016) to estimate the radial profile of sap velocity across the sapwood conducting area. These adjustments were relatively minor as sapwood thickness rarely exceeded the length of the probe by more than 0.5 cm.

We also calculated an annual estimate of water use efficiency (WUE) as the quotient of current annual increment (CAI, kg stem biomass y^{-1} , based on biomass equations in Binkley et al., 2017) and annual tree water use ($m^3 y^{-1}$) as quantified above for each clone at all sites and treatments. Tree diameter was measured every three months when



Fig. 2. Canopy (above) and stand (below) images of the high productivity clone A1 (left) and the drought resistant C3 clone (right).

probes were moved. We also examined the response of transpiration to air saturation deficit for each clone. We limited our analysis to periods where PAR was greater than $900 \mu\text{mol m}^{-2} \text{s}^{-1}$ to minimize the effect of light on stomatal conductance.

2.1. Statistical analyses

We assessed differences in water use and water use efficiency between clones and treatments within and across sites with a Generalized Linear Mixed Model (GLMM) fit to the data where a gamma-distributed response was assumed. Potential standard error bias from temporal autocorrelation in repeated measures of each tree was addressed using a residual or R-side compound symmetry error dependence structure. A test of homogeneity of covariance parameters revealed unequal variance among treatment levels ($p = 0.02$). Therefore, a residual random effect was included in the model that provided for separate variance estimates among all the treatment levels. The error degrees of freedom was calculated using the [Kenward-Roger method \(1997\)](#). Targeted comparisons between specified treatment levels was done by constructing linear contrasts and were adjusted for family-wise error by using the Sidak method ([Sidak, 1967](#)). Multiple comparisons were adjusted for family-wise error by using the Tukey-Kramer method ([Kramer, 1956](#)). We assessed differences in the transpiration response to VPD using GLMM where fixed effects included *D*, Clone and a *D**Clone interaction term and calculated the error degrees of freedom as above. GLMM analyses were performed using SAS software, copyright © 2019 SAS Institute Inc.

3. Results

3.1. Water use – Differences between clones and treatments

Our first hypothesis predicted that tree water use would be lower for the drought resistant clone however the C3 clone used 23% more water than the high productivity A1 clone at the dry site ($3.7 \text{ m}^3 \text{ y}^{-1}$ versus $3.0 \text{ m}^3 \text{ y}^{-1}$, [Fig. 3](#)) and water use was similar between the C3 and A1 clones at both the mesic and wet sites. Rain reduction appeared to lower tree transpiration for the C3 and A1 clones at the dry site by 14 to 20%, but the differences were not statistically significant ($p > 0.15$). Although annual water use did not differ between control and rainfall reduction treatments for either clone at the dry and mesic sites, there were some monthly differences and in general differences were greater for the A1 compared to the C3 clone and weakly supports our third hypothesis. At a subannual timescale, rain reduction treatments at the dry site did lower transpiration in the driest, hottest months (July, August and September 2017) for the A1 clone by 25 to 32%. Rainfall reduction led to lower water use by the drought resistant C3 clone for only one month (an 18% decrease in July, [Fig. 4](#)). Similar to the dry site, rainfall reduction did not significantly alter annual transpiration for either clone at the mesic site but there were some monthly differences. The A1 clone transpired less water (24–26%) in the rainfall reduction treatment at the mesic site during July, August and September. The C3 clone transpired 18 and 20% less water in the rainfall reduction treatment during August and September 2016 and 28% more water during May and June 2017. Annual tree water use was 59% lower in the rainfall reduction treatment for the A1 clone at the wet site and

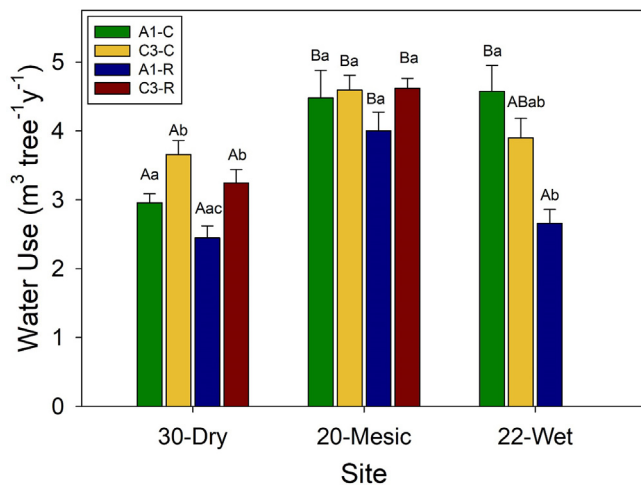


Fig. 3. The drought resistant clone C3 transpired as much or more water than the A1 clone across all three sites. C and R notations in the legend represent Control and Rainfall reduction treatments for the A1 and C3 clone. Different upper letters represent differences between sites and different lowercase letters represent significant differences within sites. Standard error bars represent the variation between trees ($n = 15$).

differences were significant for every month of measurement except for June 2017. Unfortunately we are unable to test the 3rd hypothesis at the wet site because there was no rainfall reduction treatment installed for the C3 clone but annual water use was much lower in the rainfall reduction treatment for the A1 clone and showed the largest reduction between treatments compared to the other two sites.

Monthly transpiration increased with precipitation at the dry site in the control treatment for both the A1 ($r^2 = 0.31$) and C3 clones ($r^2 = 0.25$), (Fig. 5). Monthly transpiration was positively correlated with precipitation for both clones in the rain reduction treatments at the dry site but the relationship was not quite significant (A1 $p = 0.07$, C3 $p = 0.15$). Monthly transpiration was not significantly correlated with precipitation across both clones and treatments at the mesic site ($p > 0.05$). Transpiration declined with increasing precipitation for the high productivity A1 clone in the control treatment at the wet site ($r^2 = 0.27$) but not for the rainfall reduction treatment. Monthly transpiration was not correlated with precipitation for the C3 clone at the wet site.

3.2. Annual transpiration - site differences

Trees on the driest site used the least amount of water, with clones averaging $3.0 \text{ m}^3 \text{ y}^{-1}$ (A1) and $3.7 \text{ m}^3 \text{ y}^{-1}$ (C3). Yearly water use for both clones was similar between the mesic and wet sites. The A1 clone averaged 4.5 and $4.6 \text{ m}^3 \text{ y}^{-1}$ at the mesic and wet sites respectively, while the C3 clone averaged 4.6 and $3.9 \text{ m}^3 \text{ y}^{-1}$ at these same sites. The

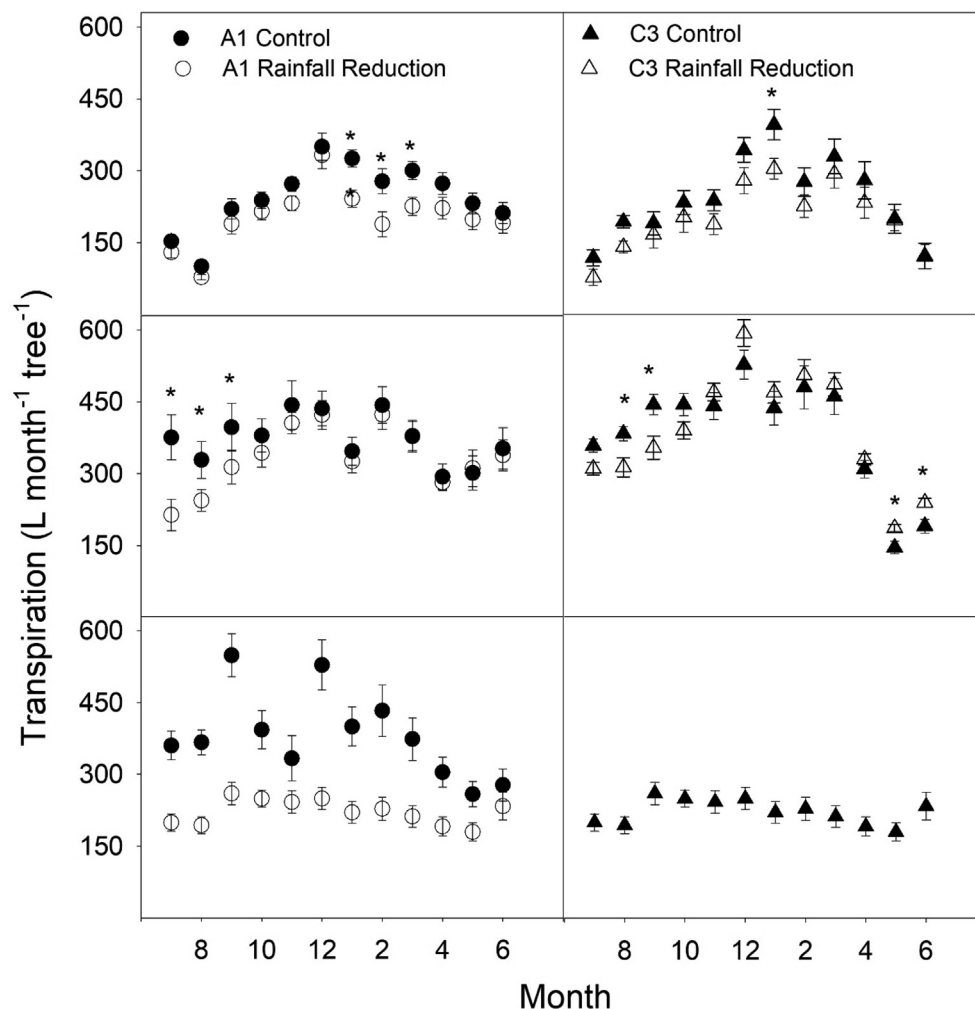


Fig. 4. Total tree transpiration per month of each clone in the control and rainfall reduction treatments at the dry, mesic and wet sites. Standard error bars represent the variation in transpiration between trees for each month ($n = 15$).

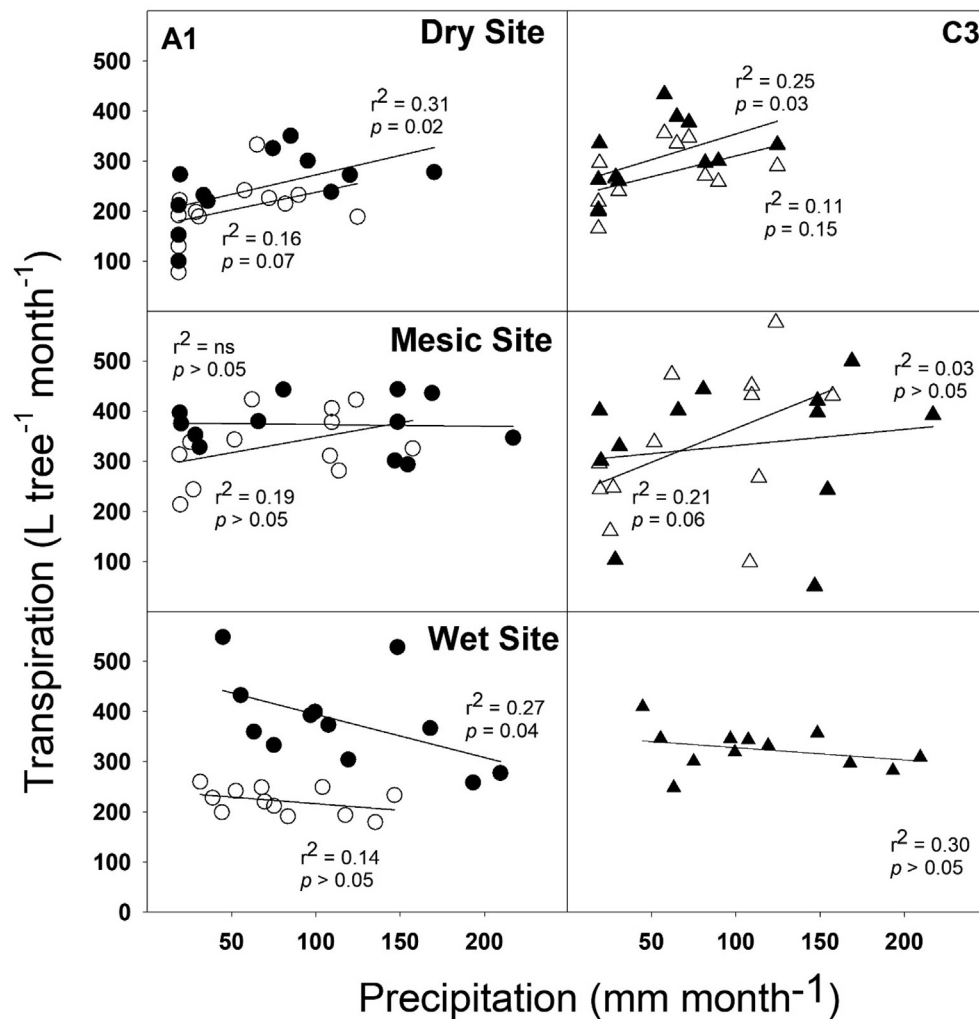


Fig. 5. Monthly transpiration response to precipitation for each clone in the control (closed symbols) and rainfall reduction treatments (open symbols) at the dry, mesic and wet sites. Standard error bars represent the monthly variation in tree water use between trees ($n = 15$).

high productivity A1 clone transpired 54, 46 and 37% of annual precipitation at the dry, mesic and wet sites respectively while the drought resistant clone C3 utilized 67, 47 and 31% of annual precipitation from the dry to the wet site (Table 1, Fig. 3).

3.3. Transpiration response to air saturation deficit

There was a distinct difference in the transpiration response to D between the drought resistant and high productivity clone in the control treatment at the dry site. Clone C3 transpired more water when D was between 2.5 and 5.25 kPa compared to the A1 clone (Fig. 6). There was a similar trend between the two clones at the mesic site but differences were not significant and the transpiration response to D was similar between the two clones at the wet site. The pattern of the transpiration versus D for clones in the rain reduction treatments was similar to the controls. The C3 clone transpired more water than A1 at high D (2.5–4.5 kPa) at the dry site as well as the mesic (1.25–3.5 kPa) site (Fig. 6).

3.4. Water use efficiency

Hypothesis two predicted water use efficiency would be higher for the drought resistant clone but we found the C3 clone had a lower WUE than A1 at the dry and mesic sites. Current annual increment was also much lower for the C3 versus A1 clone at the dry (6.3 versus 14.7 kg

y^{-1}) and mesic site (6.3 versus 21.2 kg y^{-1} , Table1). C3 had significantly lower WUE than the high productivity clone in the control treatments at the dry and mesic sites respectively (5.3 versus 1.7 kg m^{-3} Fig. 7). WUE did not differ in the control treatments between the C3 and A1 clones at the wet site. As with water use, the rainfall reduction treatments did not have a large impact on WUE for either clone and in general, differences in WUE were not significant. The exception was at the mesic site where WUE was slightly lower for the drought resistant clone C3 in the control (1.3 kg m^{-3}) versus the rainfall reduction (1.6 kg m^{-3}) treatment.

4. Discussion

Drought resistant clones might be expected to use water more conservatively than other clones, but this expectation was not correct for this experiment. The drought resistant C3 clone used as much or more water across all three sites, refuting the first hypothesis. At the driest site, the drought resistant C3 clone transpired a significantly larger percentage of yearly precipitation (67%) than the faster-growing clone A1 (54%). Although transpiration rates were similar to those found in other *Eucalyptus* forests (Morris et al., 1998; Almeida et al., 2016; Ouyang et al., 2018) there are no studies that we are aware of comparing direct measurements of tree water use for clones with contrasting drought sensitivities at the same site. A recent study however highlights the potential impact of drought resistant clones on water

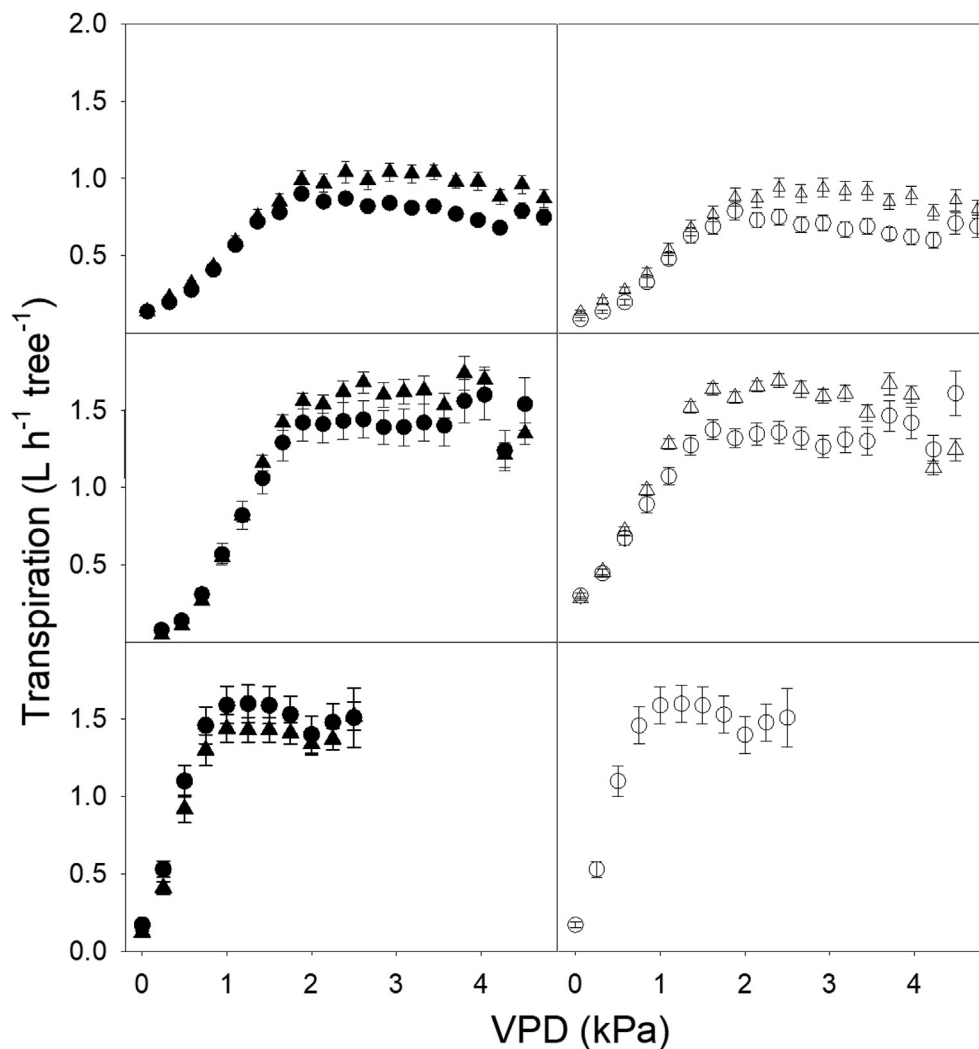


Fig. 6. Transpiration response of the A1 (●) and C3 (▲) clone (to air saturation deficit ($PAR > 900 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the control (left panels, closed symbols) and rainfall reduction treatments (right panels, open symbols) at the dry, mesic and wet sites. Standard error bars represent the variation in transpiration between trees within each VPD class ($n = 15$).

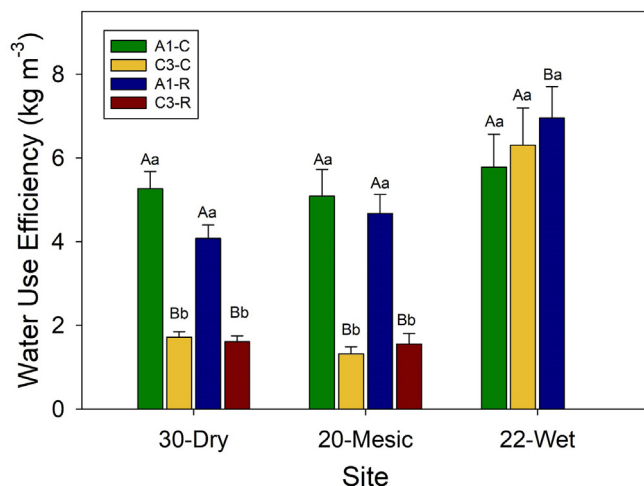


Fig. 7. Annual water use efficiency for each clone within the control and rainfall reduction treatments at each site. C and R notations in the legend represent control and rainfall reduction treatments for the A1 and C3 clone. Different uppercase letters represent differences between sites and different lowercase letters represent significant differences within sites. Standard error bars represent the variation between trees ($n = 15$).

resources; Ferraz et al. (2019) showed that evapotranspiration in *Eucalyptus* plantations can exceed 90% of precipitation in drier regions of Brazil and have a more negative impact on streamflow compared to areas with higher water availability. Our results further suggest that the decision to plant drought resistant clones in water limited areas could potentially negatively impact water resources depending on the drought resistant mechanisms of the clone.

4.1. Why did the drought resistant clone use more water?

Drought resistant plants avoid or tolerate a lack of adequate water supply by several mechanisms. Some plants drop leaves to reduce transpirational surface area while others tightly regulate stomatal conductance to avoid water loss that could lead to desiccation. Carbon allocation to roots might also be increased to access more water and there are several lines of evidence to suggest the drought resistant C3 clone does allocate more carbon belowground than the A1 clone. The C3 clone is a *E. grandis* × *E. camaldulensis* hybrid; *E. camaldulensis* depends on access to ground water in its native Australia (Nolan et al., 2018) and *E. camaldulensis* clones have been shown to have deeper root development allowing them to maintain positive growth under drought conditions (Reis et al., 2006 as cited in; Dvorak, 2012). Campoe et al. (2020) found that the C3 clone allocated about 10% more of annual

GPP below ground at the dry and mesic sites while Basillo et al. (*in prep*) found that clone C3 rooted more deeply (average of 9.5 m) than clone A1 (6.8 m average) at all three sites in this study. Deeper roots and increased carbon allocation for the C3 compared to A1 clone suggests that the C3 clone may have had access to deeper soil water reserves that facilitated transpiration rates that were higher or similar to the A1 clone. The extent that other traditional drought resistant clones can access deeper soil water deserves further investigation and will be important in furthering our understanding drought tolerance mechanisms for these clones.

Other factors may have also contributed to the high transpiration rates we observed in the C3 clone. A related study at the same sites showed that the C3 clone had a lower turgor loss point than the A1 clone during a dry period (Conti et al., 2020). A lower turgor loss point allows plants to maintain a higher stomatal conductance and lower leaf water potentials during periods of increased water demand (Bartlett et al., 2012). Further, the C3 clone has stomata on both leaf surfaces (amphistomatous) as well as steep leaf angles compared to the A1 high productivity clone. There are numerous advantages and costs of amphistomaty in plants (see review by Drake et al., 2019) but the role this leaf morphology plays in *Eucalyptus* clone productivity and water use is unclear. However, Buckley et al. (2017) found that modeled differences in surface temperatures between shaded and sunlit leaf surfaces were substantial while King (1997) showed that steep leaf angles in *Eucalyptus* species may reduce radiation load during midday and also allow plants to take advantage of low sun angles and continue photosynthesis during early morning and afternoon when atmospheric demand is low. Mattos et al. (2020) found that clone A1 has a mean leaf inclination angle of 30°, while clone C3 has mean leaf inclination angle of 65°. In addition, they showed that clone C3 has a light usage efficiency 12% higher than clone A1, 1.8 and 1.6 g MJ⁻¹ respectively. These physiological and morphological characteristics likely led to the consistently higher transpiration versus *D* patterns we observed for the C3 compared to the A1 clone (Fig. 6).

Higher water use by the C3 clone contributed to lower WUE than for the A1 clone at the dry and mesic site (Fig. 7). With abundant water availability at the wet site, the WUE did not differ between clones. The C3 clone had the highest mean annual increment at the wet site compared to all other site treatment and clone combinations which led to a high WUE at this site. Our estimates of WUE for C3 at the dry and mesic sites do not support our second hypothesis, i.e. that the drought resistant clone would be more water use efficient. We suspect that this is at least in part due to the drought resistant mechanism employed by which C3 allocates a greater proportion of GPP below ground. Other factors may also have reduced WUE for the C3 clone. Insect damage was evident on C3 leaves at the mesic site which may have decreased photosynthesis and leaf area contributing to a reduction in GPP and hence WUE during the last two months of our experiment. However in contrast, leaf damage also likely resulted in lower C3 transpiration rates during May and June 2017 (Fig. 5) suggesting that annual water use for the C3 clone may have been underestimated leading to slightly higher estimates of WUE. Unfortunately we do not have the data to quantify the importance of these factors on WUE estimates at the mesic site.

5. Conclusions and implications

The drought resistant C3 clone used as much or more water than the high productivity A1 clone across the dry, mesic and wet sites we studied. Water use efficiency for the C3 clone was also lower than A1 at the dry and mesic site. If the C3 clone we studied is similar to other drought resistant *Eucalyptus* clones in Brazil, our results suggest that decisions to plant drought resistant clones in drought prone areas should be carefully considered. This may be particularly true for coppice management systems. If drought resistant clones allocate more resources below ground to avoid drought, coppiced trees may use more water early in the rotation compared to newly planted trees. Our results highlight the

need for more research on the relative water use of drought resistant versus higher productivity clones as well as the mechanisms of drought tolerance employed by these clones.

CRedit authorship contribution statement

Robert M. Hubbard: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing - original draft, Writing - review & editing. **Rafaela Lorenzato Carneiro:** Conceptualization, Investigation, Methodology, Resources, Supervision. **Otavio Campoe:** Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Supervision, Writing - review & editing. **Clayton A. Alvares:** Project administration, Methodology, Writing - review & editing. **Marco Aurélio Figura:** Funding acquisition, Methodology, Project administration, Resources, Writing - review & editing. **Gabriela Gonçalves Moreira:** Funding acquisition, Project administration, Resources, 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.

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References

- Albaugh, J.M., Dye, P.J., King, J.S., 2013. *Eucalyptus* and Water Use in South Africa. *Int. J. Forestry Res.* 2013, 1–11.
- Almeida, A.C., Smethurst, P.J., Siggins, A., Cavalcante, R.B.L., Borges, N., 2016. Quantifying the effects of *Eucalyptus* plantations and management on water resources at plot and catchment scales. *Hydrol. Process.* 30, 4687–4703.
- Barkhordarian, A., Saatchi, S.S., Behrangi, A., Loikith, P.C., Mechoso, C.R., 2019. A recent systematic increase in vapor pressure deficit over tropical South America. *Sci. Rep.* 9.
- Bartlett, M.K., Scoffoni, C., Sack, L., 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol. Lett.* 15, 393–405.
- Berdanier, A.B., Miniat, C.F., Clark, J.S., 2016. Predictive models for radial sap flux variation in coniferous, diffuse-porous and ring-porous temperate trees. *Tree Physiol.* 36, 932–941.
- 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.
- Binkley, D., Campoe, O.C., Alvares, C., 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. *For. Ecol. Manage.* 462, 117953.
- Bosch, J.M., Hewlett, J.D., 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapo-transpiration. *J. Hydrol.* 55, 3–23.
- Buckley, T.N., John, G.P., Scoffoni, C., Sack, L., 2017. The sites of evaporation within leaves. *Plant Physiol.* 173, 1763–1782.
- Caldeira, D.R.M., Alvares, C.A., Campoe, O.C., Hakamada, R.E., Guerrini, I.A., Cegatta, I.R., Stape, J.L., 2020. Multisite evaluation of the 3-PG model for the highest phenotypic plasticity *Eucalyptus* clone in Brazil. *For. Ecol. Manage.* 462, 117989.
- Campoe, O., Ryan, M.G., Carneiro, R.O., Stape, J.L., Binkley, D., 2020. Climate and genotype influences on carbon fluxes and partitioning in *Eucalyptus* plantations. *For. Ecol. Manage.* 462, 117989.
- Clearwater, M.J., Meinzer, F.C., 2001. Relationships between hydraulic architecture and leaf photosynthetic capacity in nitrogen-fertilized *Eucalyptus grandis* trees. *Tree Physiol.* 21, 683–690.
- Conti, J.L.F., de Araujo, M.J., de Paula, R.C., Queiroz, T.B., Hakamada, R.E., Hubbard, R. M., 2020. Quantifying turgor loss point and leaf water potential across contrasting *Eucalyptus* clones and sites within the TECHS research platform. *Forest Ecol. Manage.* 462, 117989.
- Drake, P.L., de Boer, H.J., Schymanski, S.J., Veneklaas, E.J., 2019. Two sides to every leaf: water and CO₂ transport in hypostomatous and amphistomatous leaves. *New Phytol.* 222, 1179–1187.

- Dvorak, W.S., 2012. Water use in plantations of eucalypts and pines: a discussion paper from a tree breeding perspective. *Int. Forestry Rev.* 14, 110–119.
- Farooq, M., Hussain, M., Ul-Allah, S., Siddique, K.H., 2019. Physiological and agronomic approaches for improving water-use efficiency in crop plants. *Agric. Water Manage.* 219, 95–108.
- Ferraz, S.F.D., Rodrigues, C.B., Garcia, L.G., Alvares, C.A., Lima, W.D., 2019. Effects of Eucalyptus plantations on streamflow in Brazil: Moving beyond the water use debate. *For. Ecol. Manage.* 453.
- Goncalves, J.L.D., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., Ferraz, S.F.D., Lima, W.D.P., Brancalion, P.H.S., Hubner, A., Bouillet, J.P.D., Laclau, J.P., Nouvellon, Y., Epron, D., 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. *For. Ecol. Manage.* 301, 6–27.
- Granier, A., 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42, 193–200.
- Hubbard, R.M., Stape, J., 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.
- Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., et al., 2018. Chapter 3: Impacts of 1.5°C global warming on natural and human systems. In: *Global Warming of 1.5 °C: An IPCC special report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. Intergovernmental Panel on Climate Change.
- Kenward, M.G., Roger, J.H., 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53, 983–997.
- King, D.A., 1997. The functional significance of leaf angle in Eucalyptus. *Aust. J. Bot.* 45, 619–639.
- Kramer, C.Y., 1956. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics* 12, 307–310.
- 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.* 464, 118038.
- Morris, J., Mann, L., Collopy, J., 1998. Transpiration and canopy conductance in a eucalypt plantation using shallow saline groundwater. *Tree Physiol.* 18, 547–555.
- Nolan, R.H., Tarin, T., Rumman, R., Cleverly, J., Fairweather, K.A., Zolfaghari, S., Santini, N.S., O'Grady, A.P., Eamus, D., 2018. Contrasting ecophysiology of two widespread arid zone tree species with differing access to water resources. *J. Arid Environ.* 153, 1–10.
- Otto, M.S.G., Hubbard, R.M., Binkley, D., Stape, J.L., 2014. Dominant clonal Eucalyptus grandis x urophylla trees use water more efficiently. *For. Ecol. Manage.* 328, 117–121.
- Ouyang, L., Zhao, P., Zhou, G.S., Zhu, L.W., Huang, Y.Q., Zhao, X.H., Ni, G.Y., 2018. Stand-scale transpiration of a Eucalyptus urophylla x Eucalyptus grandis plantation and its potential hydrological implication. *Ecophysiology* 11.
- 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.
- Sidak, Z., 1967. Rectangular confidence regions for means of multivariate normal distributions. *J. Am. Stat. Assoc.* 62.
- Stape, J.L., Binkley, D., Ryan, M.G., 2004. Eucalyptus production and the supply, use and efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. *For. Ecol. Manage.* 193, 17–31.
- Ullah, H., Santiago-Arenas, R., Ferdous, Z., Attia, A., Datta, A., 2019. Improving water use efficiency, nitrogen use efficiency, and radiation use efficiency in field crops under drought stress: A review. In: Sparks, D.L. (Ed.), *Advances in Agronomy*, Vol 156, pp. 109–157.