



Dominant clonal *Eucalyptus grandis* × *urophylla* trees use water more efficiently



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ABSTRACT

Wood growth in trees depends on the acquisition of resources, and can vary with tree size leading to a variety of stand dynamics. Typically, larger trees obtain more resources and grow faster than smaller trees, but while light has been addressed more often, few case studies have investigated the contributions of water use and water use efficiency (WUE) within stands to isolate the tree-size dominance effect. Our sites were located near the cities of Aracruz and Eunapolis in Northeastern Brazil. We measured tree biomass growth, water use and WUE to explore patterns of growth among dominant and non-dominant trees in rainfed (1350 mm yr⁻¹) and irrigated experimental stands in two high productivity tropical clones of *Eucalyptus grandis* × *urophylla* growing in clayey Ultisol soils. During the study period, irrigation supplied an additional 607 mm and 171 mm at the Aracruz and Eunapolis sites respectively. We tested two hypotheses; (1) larger trees transpire more water, and produce more wood per water used (higher water use efficiency, WUE) than smaller trees of the same clone and; (2) this pattern also applies if a water surplus is added via irrigation to alleviate water stress.

Across both sites, we measured stand water use using sap flow sensors from August to December, and quantified wood growth on a tree-basis and then derived WUE, in kg wood per m³ of water transpired. Dominant trees showed higher rates of tree growth, water use and WUE than dominated trees for the two sites-clones and under both water supply regimes. Using the rainfed trees at Aracruz as an example, 50-kg trees grew 1.0 kg month⁻¹ compared with growth of 100-kg trees of 3.8 kg month⁻¹. The smaller trees would use water in a rate of 2.1 m³ month⁻¹, compared with 3.1 m³ month⁻¹ for the larger trees, demonstrating a higher WUE for the larger tree (1.2 kg m⁻³ versus 0.5 kg m⁻³). Our results suggest that manipulating stand density on heterogeneous stands, e.g. thinning, has the potential to minimize the tradeoffs between wood growth and tree water use in *Eucalyptus grandis* × *urophylla* plantations, mainly in tropical regions with seasonal water deficit. However, more research is needed to discern the underlying mechanisms responsible for higher WUE exhibited by dominant trees and distinct clones.

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1. Introduction

Variation in sizes among trees within stands leads to a variety of stand dynamics, typically involving positive feedbacks of larger trees obtaining more resources and growing faster than smaller trees, leading to further increases in variation in tree sizes. Stand-level production may also be influenced by the variation of

tree size. For example, Stape et al. (2010) found that increasing heterogeneity of tree sizes in monoclonal stands of *Eucalyptus* lowered stand-level production from 10% to 18%.

Larger trees may also grow faster than smaller trees in the same stand by using resources more efficiently in producing wood (Binkley et al., 2004). A recent issue of *Forest Ecology and Management* examined patterns of light use and the efficiency of light use by individual trees within stands and found that both factors were often important for explaining faster growth of larger trees (Binkley et al., 2013). However fewer case studies have investigated the contributions of water use and water use efficiency in accounting for variation in tree growth rates within stands.

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Binkley et al. (2002) reported that the largest 25% of trees in a plantation of *Eucalyptus saligna* in Hawaii accounted for 50% of stand-level water use and 60% of stand growth, reflecting greater water use efficiency in larger trees. Gyenge et al., 2008 found that Douglas-fir and native tree species showed higher water use efficiencies for larger trees within stands. Fernandez and Gyenge (2009) examined stands of ponderosa pine of varying densities at two sites in Argentina: water use was consistently greater for larger, faster-growing trees, but higher efficiency of water use by larger trees was apparent at only one site. Forrester et al. (2012) found that larger *Eucalyptus nitens* trees showed slightly greater water use efficiency (across a variety of stand treatments) than smaller trees. In all these cases, there is a confounded genetic-size effect for the tree classes, due to the seed origins of the plantations. So, a smaller tree can present a lower WUE due to its lower genetic quality or size, making clonal *Eucalyptus* plantations ideal to address specifically the water use and WUE for non-dominant and dominant trees.

A variety of studies has examined stand-level water use, examining the importance of species (Sala et al., 1996; Salama et al., 1994; Kostner et al., 1992; White et al., 2002), fertilization (Ewers et al., 1999; Phillips et al., 2001; Hubbard et al., 2004), and irrigation (Myers and Talsma, 1992; Hubbard et al., 2010). The patterns of individual-tree water use within stands have not been examined in relation to tree sizes; are dominant trees more or less efficient at using water to produce wood? More case studies are needed to determine the general patterns of within-stand water use and efficiency of use as a foundation for general understanding of common trends and factors driving variation around the trends. We tested two hypotheses about variation in water use and efficiency with tree size in two clonal plantations of *Eucalyptus grandis* × *urophylla* in Brazil:

1. Larger trees transpire more water and produce more wood per water used (higher WUE) than smaller trees of the same clone;
2. This pattern also applies if a water surplus is added via irrigation to alleviate water stress.

The distinction between water use and efficiency of water use for trees of varying sizes is particularly relevant to selection of planting densities, thinning, stand uniformity, and response to drought. If non-dominant trees use water less efficiently than dominant trees, then higher densities and greater variations in tree sizes would lead to stand-level reductions in the efficiency of water use and possibly increase drought stress. And in a regional approach, more water will be transpired to produce the same amount of a desired wood production, leading to more planted area and less available water for rural and urban areas.

2. Methods

We conducted our experiment in two experimental plantations that were part of the Brazil *Eucalyptus* Potential Productivity (BEPP) study (Stape et al., 2010). The Aracruz site is located in the state of Espírito Santo (19° 49' S, 40° 05' W), had a 6-year-rotation wood net primary production (WNPP) of 18.3 Mg ha⁻¹ yr⁻¹ without irrigation, and 28.2 Mg ha⁻¹ yr⁻¹ with irrigation. The Eunapolis site in the state of Bahia (16° 21'S, 39° 34'W) had a WNPP of 29.8 Mg ha⁻¹ yr⁻¹ without irrigation, and 35.8 Mg ha⁻¹ yr⁻¹ with irrigation. Both sites had a similar clayey Ultisol soil types, mean annual temperature (23.6 °C), average precipitation (1390 mm yr⁻¹), average potential evapotranspiration (1200 mm yr⁻¹) and vapor pressure deficit (0.78 kPa). The sites' climate are classified as an Af/Am under Koppen Classification (Alvares et al., 2013) showing a somewhat uniform rainfall

distribution, allowing for a half-year study length. Water-use measurements for this study occurred in the fifth year of the rotation from August to December 2005, when both sites received about 610 mm of rain. Trees were planted in an uniform 3 m × 3 m spacing (1111 trees ha⁻¹). Plot size for all treatments was 10 × 10 trees (30 × 30 m) with a 6 × 6 trees interior measurement plot. Site specific *Eucalyptus grandis* × *urophylla* clonal stock was supplied by each company and planted in 2001 (Clones ARA3918 and VER43 for Aracruz and Eunapolis, respectively). Although both materials are *E. grandis* × *urophylla* hybrids, they have intrinsically distinct genetic potentials. Marrichi (2009) studied both clones together in Piracicaba, Sao Paulo State, and at year 3, Veracel clone was 22% more productive than the Aracruz clone.

The overall BEPP experiment included three replicate plots at Aracruz and four replicates at Eunapolis. Irrigated and rainfed plots at each site received identical applications of fertilizer to separate the effects of nutrition and irrigation (Stape et al., 2010). For irrigated treatments, water was applied with drip hose distributed evenly among the trees and supplied to compensate for evapotranspiration, leading to an additional 607 mm at Aracruz and 171 mm at Eunapolis during the study period.

Sap flux density (v , g cm⁻² s⁻¹) was determined using 2-cm Granier-style heat dissipation probes. Trees were instrumented in one irrigated and one rainfed plot at each site, with 18 irrigated trees and 18 rainfed trees at Aracruz, and 6 irrigated trees and 7 rainfed trees at Eunapolis. Details of the measurement techniques are given in Hubbard et al., 2010. Briefly, we assumed probes measured an integrated instantaneous sap velocity over the average sapwood thickness (Fig. 1) for instrumented trees at the Aracruz (2.0 ± 0.05 cm) and Eunapolis (2.5 ± 0.04 cm) respectively. Probe placement was randomly selected for each tree to minimize variation in sapflux density with circumference and probes were moved



Fig. 1. Instrumented trees at the Aracruz site (upper, clone ARA3918, 38 m³ ha⁻¹ yr⁻¹) and Eunapolis site (lower, clone VER43, 60 m³ ha⁻¹ yr⁻¹) at 5 yr-old in Brazil and visualization of sapwood thickness and area for VER43.

approximately every 3 months to minimize wounding effects and overgrowth of probes by rapid diameter growth. More frequent repositioning of the probes was not necessary as tree growth did not significantly overgrow probes and moving probes often causes damage that results in probe failure. For this study, probes were moved once for each tree and which did not significantly impact instantaneous sapflux density for each tree. Probes were insulated from thermal gradients using a closed cell foam block and foil backed insulation (Fig. 1) reflecting 96% of incoming radiant energy (Reflectix Inc., Markleville, IN). Probes and insulation were protected from moisture and stemflow using plastic sheeting. Probes were connected to datalogger equipped with a multiplexer (CR10x and AM16/32, Campbell Sci. Inc., Logan, UT) and 15 s instantaneous v measurements were averaged and recorded every 15 min.

Tree growth was calculated based on the change in diameter and height over this interval, with locally developed regression equations (Stape et al., 2010). Sapwood area at the measurement point (Fig. 1) was calculated using allometric equations developed at each site. Sapwood area was estimated from harvested trees (70 irrigated and 21 rainfed at Aracruz, 54 irrigated and 20 rainfed at Eunapolis; Hubbard et al., 2010). Water use was calculated as the product of sapwood area and sapflux density for each 15 min period and summed to estimate total water use per month. Water use efficiency was calculated as the average monthly stem biomass increment for each tree divided by monthly average water use.

We examined trends in growth, water use, and growth per unit water use (water use efficiency) as a function of tree size using CurveExpert 2.0.3 (<http://www.curveexpert.net>), and AICc (Akaike's Information Criterion corrected for finite sample size; Burnham and Anderson, 2002) to determine the best fit.

3. Results and discussion

Tree growth increased exponentially with tree size at the Aracruz site and linearly at Eunapolis (Fig. 2A and B). Interestingly, trees less than about 125 kg (about 17 cm diameter at breast height) showed higher growth in rainfed plots than in irrigated plots. This likely reflects tree dominance patterns; this size tree was dominant in rainfed plots, but only average-sized in the irrigated plots.

Water use increased linearly with tree size for both sites and both water supply regimes (Fig. 2C and D). Rainfed trees at Aracruz used more water for a given size tree than did irrigated trees; this again reflects the large differences in the size of the dominant (high water use) trees between the treatments.

Larger trees not only used more water than smaller trees, they produced more wood per unit of water used. Water use efficiency increased exponentially for rainfed and irrigated treatments at both sites (Fig. 3).

Both hypotheses were strongly supported by the experiment. Using the rainfed trees at Aracruz as an example, 50-kg trees averaged an increment of $1.0 \text{ kg month}^{-1}$ (Fig. 2A) and 100-kg trees averaged $3.8 \text{ kg month}^{-1}$ (Fig. 2A). The smaller trees would use $2.1 \text{ m}^3 \text{ month}^{-1}$, compared with $3.1 \text{ m}^3 \text{ month}^{-1}$ for the larger trees. The proportional difference in growth (3.8-fold) was greater than the proportional difference in water use (1.5-fold), demonstrating a higher water use efficiency for the larger tree (1.2 kg m^{-3} versus 0.5 kg m^{-3}). Forrester et al. (2012) found that the largest *Eucalyptus nitens* trees were 7% more efficient than the smallest trees, and that stem-wood growth was highly correlated with transpiration. About 40% of the greater growth for the larger trees in their study resulted from higher water use, and 60% resulted from higher water use efficiency.

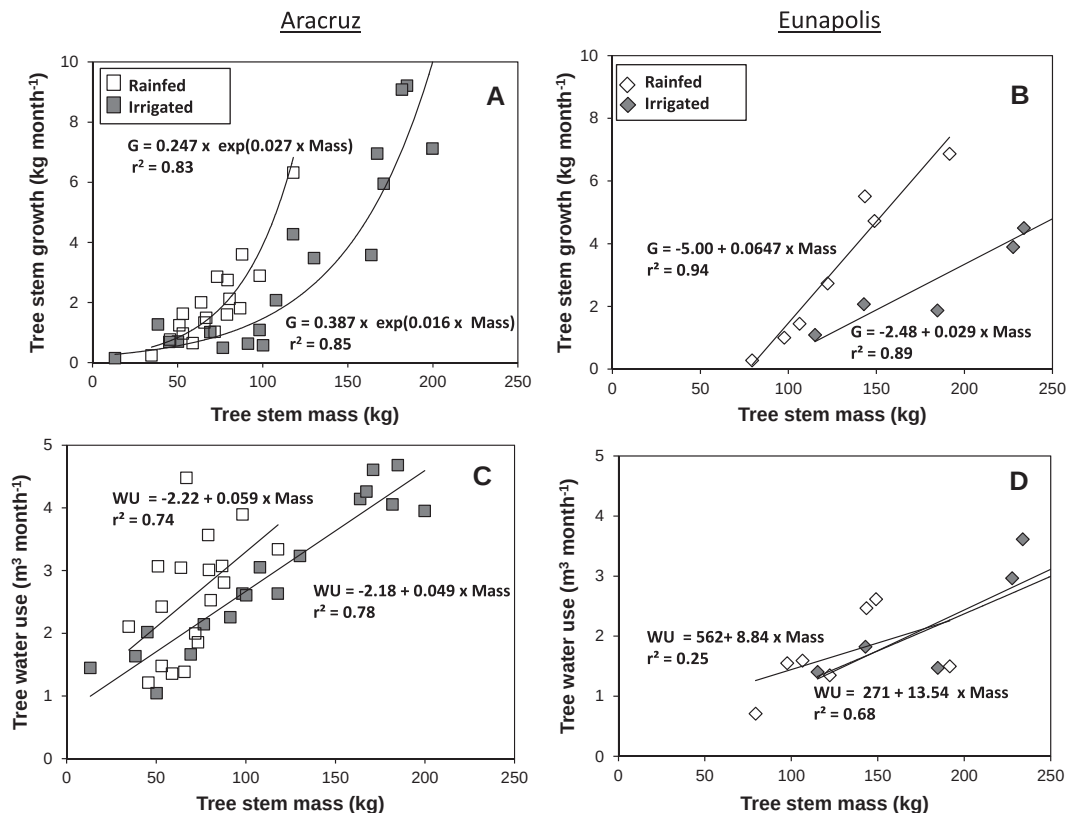


Fig. 2. Growth (G) increased with increasing tree size (A and B), as did water use (WU) (C and D). The patterns were consistent across both rainfed and irrigated treatments. ($P < 0.05$ for all lines and curves.)

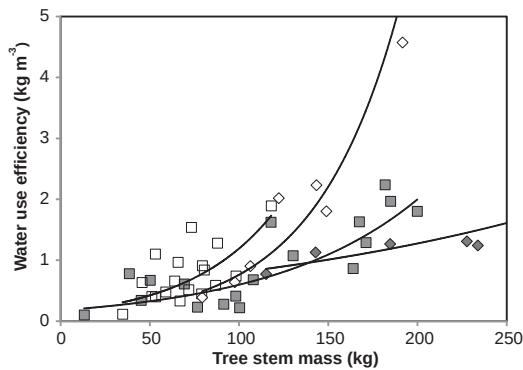


Fig. 3. Water use efficiency increased with tree size at both sites-clones, with and without irrigation. Squares are for Aracruz (rainfed open squares $WUE = 0.206 \times \exp(0.018 \times \text{mass})$, $r^2 = 0.44$; irrigated filled squares ($WUE = 0.223 \times \exp(0.011 \times \text{mass})$, $r^2 = 0.71$). Diamonds are for Eunapolis (rainfed open diamonds $WUE = 0.162 \times \exp(0.017 \times \text{mass})$, $r^2 = 0.94$; irrigated filled diamonds $WUE = 0.485 \times \exp(0.005 \times \text{mass})$, $r^2 = 0.70$). ($P < 0.05$ for all lines and curves.)

Errors in estimating sapflux across the entire radial sapwood profile could potentially influence our results. However, we argue that these errors would be in a direction that would further support our hypotheses. For example, in smaller trees, a small portion of our 2 cm probes may have been in nonconductive heartwood tissue. If so, correcting for this error would increase our estimates of tree water use (e.g. Clearwater et al., 1999) and water use efficiency would be lower than we reported in Fig. 2. Conversely, if our 2 cm probes were not long enough to measure the entire sapwood radial profile in large trees, correcting for this error would decrease our estimates of large tree water use (e.g. James et al., 2002) and water use efficiency would be higher than reported in Fig. 2. Our estimates of the differences in water use efficiency across tree sizes therefore offer conservative support of our hypotheses.

The factors responsible for higher water use efficiency by larger, dominant trees warrants direct measurement and experimentation. Larger trees may have higher rates of photosynthesis per unit of leaf area or light absorption, but differences in photosynthetic rates are likely too small to account for the majority of the difference in water use efficiency. Indeed, these two clones did not differ in photosynthetic rates for the whole canopy at 1.5 and 3.0 yr-old when planted at the same site (Marrichi, 2009). Standard deviations among trees within stands tend to be about 5–10% of the mean for well-lit leaves on fast-growing *Eucalyptus* trees (e.g., Battaglia et al., 1996; Lewis et al., 2011). This is an order of magnitude smaller than the differences in water use efficiency among

tree sizes in Fig. 3. Another consequence of the observed trend shown in Fig. 3 is that, at least up to the replacement of the potential evapotranspiration, *Eucalyptus* clones do not just transpire water without coupling it to carbon fixation. This implies that there is no waste of water from the system under a wood production point of view, and the tree-level knowledge can potentially lead to more efficient forest practices.

Larger trees might allocate a smaller fraction of total photosynthates to belowground production, leaving a greater fraction for use in growing stems. Stape et al. (2008) found a decrease in the below carbon allocation from 34% of the Gross Primary Production (GPP) to 28% of the GPP when a tropical *Eucalyptus grandis* × *urophylla* clones was irrigated in Northeastern Brazil, but there was no tree-basis evaluation. A similar trend was observed by Ryan et al. (2010) for the BEPP study. At the tree-level, this idea remains challenging to test under realistic field conditions, however, as no method has been developed to measure the below-ground production of individual trees within a stand (Binkley et al., 2006).

At a stand level, smaller trees consume substantial amounts of water but provide little growth. For example, the smallest trees that used one-third of total water use at the Aracruz site provided less than 20% of total growth. The largest trees accounting for one-third of total water use provided more than 50% of total growth (Fig. 4A and B). If the smaller, low-efficiency trees were removed from the stand, the remaining trees would have substantially greater amount of water supply. For example, Forrester et al. (2012) found that approximately 3 yr after thinning an *E. nitens* stand, the remaining large trees had about 22% higher transpiration rates relative to large trees in unthinned stands. If the increased water supply could be used by the larger residual trees, and these trees retained their higher efficiency of water use, then stand growth should drop by a smaller amount than expected after thinning the smaller trees based on the relative removal of biomass. Considering different thinning from below intensities, differences in WUE among tree-size classes and genetics, no-drop in stand growth is theoretical possible. We are wary of this reasoning, however, because thinning from below does not generally increase stand growth. For example, West and Osler (1995) found thinning did not increase production in a *Eucalyptus regnans* stand because an increase in belowground resources was not sufficient to overcome the reduction in light absorption resulting from the reduction in leaf area. Similarly, Hocker (1982) found that, four years after thinning, above ground biomass was less in thinned plots compared with unthinned plots for *Populus tremuloides* because leaf area index was still substantially less than unthinned stands.

The lack of increase in stand-level growth after thinning implies either that the residual stand fails to fully sustain total water use

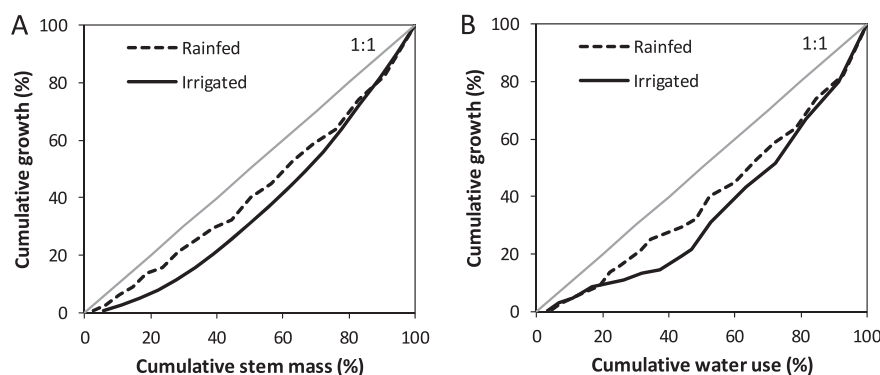


Fig. 4. Trees for the Aracruz site were ranked from smallest to largest. The 1:1 line would indicate all trees contributed proportionally to both biomass and growth (A); the curves fall below this line indicating the larger trees contributed a disproportionate amount of stand growth. The same pattern was evident for tree growth as a function of cumulative water use; the curves fall below 1:1, indicating substantially higher efficiency of water use for larger trees.

(e.g. due to the decrease in leaf area index), or the efficiency of residual trees in fact drops after thinning (e.g. due to change in the microclimatic conditions). Detailed experiments that quantify changes in soil moisture, tree water use and leaf/canopy gas exchange across stand densities for distinct clonal materials or following thinning would increase our understanding the actual dynamics of tree water use and efficiency.

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