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Effects of irrigation on water use and water use efficiency in two fast growing *Eucalyptus* plantations

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ABSTRACT

Eucalyptus plantations occupy almost 20 million ha worldwide and exceed 3.7 million ha in Brazil alone. Improved genetics and silviculture have led to as much as a three-fold increase in productivity in *Eucalyptus* plantations in Brazil and the large land area occupied by these highly productive ecosystems raises concern over their effect on local water supplies. As part of the Brazil Potential Productivity Project, we measured water use of *Eucalyptus grandis* × *urophylla* clones in rainfed and irrigated stands in two plantations differing in productivity. The Aracruz (lower productivity) site is located in the state of Espirito Santo and the Veracel (higher productivity) site in Bahia state. At each plantation, we measured stand water use using homemade sap flow sensors and a calibration curve using the clones and probes we utilized in the study. We also quantified changes in growth, leaf area and water use efficiency (the amount of wood produced per unit of water transpired). Measurements were conducted for 1 year during 2005 at Aracruz and from August through December 2005 at Veracel. Transpiration at both sites was high compared to other studies but annual estimates at Aracruz for the rainfed treatment compared well with a process model calibrated for the Aracruz site (within 10%). Annual water use at Aracruz was 1394 mm in rainfed treatments versus 1779 mm in irrigated treatments and accounted for approximately 67% and 58% of annual precipitation and irrigation inputs respectively. Increased water use in the irrigated stands at Aracruz was associated with higher sapwood area, leaf area index and transpiration per unit leaf area but there was no difference in the response of canopy conductance with air saturation deficit between treatments. Water use efficiency at the Aracruz site was also not influenced by irrigation and was similar to the rainfed treatment. During the period of overlapping measurements, the response to irrigation treatments at the more productive Veracel site was similar to Aracruz. Stand water use at the Veracel site totaled 975 mm and 1102 mm in rainfed and irrigated treatments during the 5-month measurement period respectively. Irrigated stands at Veracel also had higher leaf area with no difference in the response of canopy conductance with air saturation deficit between treatments. Water use efficiency was also unaffected by irrigation at Veracel. Results from this and other studies suggest that improved resource availability does not negatively impact water use efficiency but increased productivity of these plantations is associated with higher water use and should be given consideration during plantation management decision making processes aimed at increasing productivity.

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1. Introduction

Eucalyptus is a widely planted tree species, occupying almost 20 million ha worldwide (Iglesias and Wistermann, 2008). In Brazil alone, land area devoted to *Eucalyptus* plantations exceeds 3.7 million ha and has doubled over the past decade. Improved genetics and intensive silvicultural practices has led to as much as a three-fold increase in productivity of Brazilian *Eucalyptus* plantations over the past 40 years, making these ecosystems some of the most productive (>40 $m^3\ ha^{-1}\ y^{-1}$ of wood) in the world (Eldridge et al., 1994; Stape et al., 2001).

The expansion of these *Eucalyptus* plantations raises concern over their effect on local water resources (Almeida et al., 2010). Rotation lengths of *Eucalyptus* plantations for pulpwood production in Brazil are on the order of 6–7 years with canopy closure typically occurring within 2–3 years of planting. Successive plantings and harvests over large areas have the potential for higher sustained transpiration rates than slower growing species.

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There is a significant amount of data indicating afforestation with *Eucalyptus* species can affect streamflow (Bosch and Smith, 1989; Scott and Lesch, 1997; Scott and Prinsloo, 2008; Silveira and Alonso, 2009) depending on rainfall intensity and distribution, soil texture, tree age and stocking (Almeida et al., 2007). Given the rapid rate of plantation expansion in Brazil, there is a need for more information on how water use by these plantations varies with forest productivity as well as management intensity.

Trees lose water to the atmosphere when stomata open to acquire CO_2 for photosynthesis such that canopy conductance ultimately determines forest water use. The past two decades have seen significant advances that have increased our understanding of the response of stomata to environmental variables and the role of the hydraulic pathway from soil to leaf in regulating stomatal conductance. Although the actual mechanism(s) by which plants control stomatal opening are still not clearly defined, research results clearly show that stomata respond to changes in environmental variables (e.g. light, humidity, soil moisture) (Franks et al., 1997; Jarvis, 1976; Oren et al., 1999; Pataki et al., 1998) as well as hydraulic properties (e.g. hydraulic conductivity and leaf area to sapwood ratios) (Hubbard et al., 2001; McDowell et al., 2002; Mencuccini, 2003; Zeppel and Eamus, 2008) thus influencing the amount of water trees use over short and long time scales. Silvicultural treatments and resource additions (fertilization and or irrigation) have the potential to alter canopy conductance, leaf area, sapwood area and the water potential gradients that exist between soil and canopy and as a result, change both the amount of water transpired and the amount of carbon assimilated during photosynthesis.

The amount of water transpired relative to the amount of stem biomass (or carbon) produced can be defined as water use efficiency of wood production (Jones, 1994; Dye, 2000). This metric directly relates productivity and consumptive water use by vegetation and has been used in many studies to examine species distributions along environmental gradients, adaptation to drought (Whitehead and Beadle, 2004) and to better understand changes in water use and growth with stand development (Almeida et al., 2007; Forrester et al., 2010). Land managers are particularly interested in water use efficiency for selection of species best suited for areas limited by water supply (Dye, 2000). There are fewer studies that have examined how water use efficiency changes with management intensity but changes in resource use and efficiency may influence land management decisions and sustainability. An understanding of the processes controlling water use and water use efficiency in *Eucalyptus* plantations is important for informed land management decisions and potentially for improved selection processes for clonal stock (Dye, 2000).

Most studies have used existing environmental gradients to assess the response of *Eucalyptus* to changes in soil water availability but these are complicated by the fact that water availability typically covaries with productivity. The Brazil *Eucalyptus* Potential Productivity Project, (BEPP) (Stape et al., 2010) allowed us to assess water use and water use efficiency at two sites with different productivities while increasing water supply in a replicated treatment. Our objective in this study was to examine the effects of irrigation on tree water use and water use efficiency in two fast growing *Eucalyptus* plantations with contrasting productivities. Within the BEPP experimental design we measured whole tree water use with Granier style sap flux probes (Granier, 1987) in rainfed and irrigated treatments. Our study was designed to answer three basic questions: (i) how does monthly and annual water use differ between rainfed and irrigated treatments; (ii) if irrigation increases stand water use, are differences caused by increases in leaf area and/or physiological changes (i.e. canopy conductance) and (iii) does increased water supply at the same site influence water use efficiency?

2. Methods

2.1. Study sites

We conducted our experiment on study sites that were a subset of the BEPP study. Among the seven forest companies providing plantation area for the BEPP study, we chose *Eucalyptus* plantations within the Aracruz and Veracel companies' land holdings that provided the widest range of wood production between sites. The Aracruz (lower productivity) site is located in the state of Espirito Santo (19°49′S, 40°05′W) and the Veracel (higher productivity) site in Bahia (16°21′S, 39°34′W) state. Both sites have similar deep (>2 m) Ultisol soil types. Aboveground net primary production (ANPP) averages 26 Mg ha^{-1} y^{-1} and 37 Mg ha^{-1} y^{-1} for the Aracruz plantation in rainfed and irrigated treatments respectively. For Veracel, ANPP was higher, averaging 38 Mg ha^{-1} y^{-1} and 44 Mg ha^{-1} y^{-1} for the rainfed and irrigated treatments. Mean annual temperature is 24 °C and average precipitation at Aracruz and Veracel is 1250 mm y^{-1} and 1180 mm y^{-1} respectively (Stape et al., 2010). However, during our study period (2005), both sites received significantly more than average precipitation (Aracruz = 2067 mm, Veracel = 1641 mm, Table 1). Meteorological data including radiation, temperature, relative humidity and wind speed were collected on site at each location by using standard meteorological stations (Stape et al., 2010).

2.2. Experimental design

As part of the larger BEPP project (for full description, see Stape et al., 2010), we utilized rainfed and irrigated treatment plots to assess our research questions. Plot size for all treatments was 30 m × 30 m with an 18 m × 18 m interior measurement plot. Each interior plot consisted of 36 trees arranged in a uniform

Table 1
Aracruz and Veracel site information, from the beginning (45 months) and end (57 months) of the study period (2005).

Treatment	Aracruz		Veracel	
	Rainfed	Irrigated	Rainfed	Irrigated
Planting date	March 2001	March 2001	March 2001	March 2001
Tree spacing (m)	3 × 3	3 × 3	3 × 3	3 × 3
Mean bole increment at 5 y (Mg ha^{-1} y^{-1})	17.5	28.2	34.1	35.5
Bole NPP plot in 2005 (Mg ha^{-1} y^{-1})	20.2	27.6	25.9	24.5
Annual precipitation and irrigation surplus 1–5 years (mm)	1360	+744	1368	+914
Precipitation and irrigation surplus in 2005 period (mm)	2067	+951	1671	+742
Mean diameter at 45 months old (cm ± s)	13.4 ± 2.1	15.4 ± 3.4	17.7 ± 2.2	18.2 ± 2.0
Mean height at 45 months old (m ± s)	18.1 ± 1.8	20.6 ± 4.1	26.0 ± 1.6	26.6 ± 1.4
Mean biomass at 45 months old (kg ± s)	54.5 ± 21.6	95.6 ± 48.4	119.4 ± 44.8	126.8 ± 47.7
Mean diameter at 57 months old (cm ± s)	14.0 ± 2.3	16.0 ± 3.5	18.6 ± 2.7	19.0 ± 2.5
Mean height at 57 months old (m ± s)	20.4 ± 2.4	22.8 ± 4.8	28.6 ± 2.3	29.1 ± 2.0
Mean biomass at 57 months old (kg/tree ± s)	72.7 ± 33.2	120.5 ± 67.9	143.2 ± 60.6	148.8 ± 62.8

3 m × 3 m spacing. Site specific *Eucalyptus grandis* × *urophylla* clonal stock was supplied by each company and planted in 2001.

Our experimental design included three replicate plots at Aracruz and four replicates at Veracel. Irrigated and non-irrigated plots at each site received identical applications of fertilizer to separate the effects of nutrition and irrigation (Stape et al., 2010). Treatments were separated by a narrow 1 m deep trench to eliminate root growth between plots and to ensure irrigation did not influence adjacent treatments. For irrigated treatments, water was applied weekly with drip hose distributed evenly among the trees and supplied an additional 951 mm at Aracruz and 741 mm at Veracel. During our study, tree diameter at breast height averaged 13.4 cm in rainfed and 15.4 cm irrigated treatments at Aracruz and 17.4 cm and 18.8 cm in rainfed and irrigated treatments at Veracel. Tree height in rainfed and irrigated treatments at Aracruz averaged 19.5 m and 21.6 m respectively, while tree height at Veracel averaged 26.6 m in rainfed and 27.8 m in irrigated treatments.

2.3. Sapwood area, leaf area index and sap flux density

Sapwood area at the measurement point was calculated using allometric equations developed at each site. At Aracruz, irrigated ($n = 70$) and non-irrigated ($n = 21$) trees were harvested from plot buffer areas. Thin (1–1.5 cm) disks were cut at breast height and conducting sapwood area was estimated visually by measuring four equally opposed radii of the obvious translucent portion of the disk and calculating area as an ellipse. Analysis of covariance (PROCMIXED, SAS) indicated no significant difference between treatments ($p = 0.18$) and treatments were combined and a single equation fit to all trees (Fig. 2). At the Veracel site, irrigated ($n = 54$) and non-irrigated ($n = 20$) trees were harvested from plot buffer areas and sapwood area determined for combined treatments as for Aracruz. Leaf area index was obtained using a plant canopy analyzer (LAI-2000, Licor, Inc.) at the Aracruz site and calibrated as in Almeida et al. (2007). A ceptometer was used to obtain LAI at Veracel using methods described by Stape et al. (2010).

Sap flux density (ν, g cm^{-2} s^{-1}) was determined using home-made 2 cm Granier style heat dissipation probes (Granier, 1987) at the Aracruz and Veracel sites. Our probes were similar to the original Granier design except they contained the heater wire on the inside of the needle as opposed to being wrapped around the outside thus facilitating movement of the sensors without damaging the heater wire. We assumed probes measured an integrated instantaneous sap velocity over the average sapwood thickness for instrumented trees at the Aracruz (2.0 ± 0.05 cm) and Veracel (2.5 ± 0.04 cm) respectively. Probes were insulated from thermal gradients using a closed cell foam block and foil backed insulation 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 a datalogger equipped with a multiplexer (CR10x and AM16/32, Campbell Scientific Inc., Logan, UT) and 15 s instantaneous ν measurements were averaged and recorded every 15 min.

Twenty trees per treatment plot were instrumented at the Aracruz site and 10 trees (due to logistical and budgetary constraints) per treatment plot were instrumented at the Veracel site. We selected trees that were greater than −1 standard deviation of the mean in order to ensure our sample size included size classes that were the largest contributors to stand transpiration. Diameters of the trees we measured at both sites represented size classes that were 98% of the above ground woody biomass and leaf area of the respective sample plots. We randomly selected an azimuth (0–359°) for a single probe location assuming that random placement partially accounted for variations in sap velocity with circumference. To further account for the variation of sap velocities associated with circumference within a single tree and to ensure rapid diameter growth did not overgrow the gauge, probes were repositioned approximately 90° every 3 months into freshly drilled holes. At Aracruz, ν was monitored from January to December 2005. At Veracel, ν was measured from August to December 2005.

2.4. Calibration

Estimates of ν using the standard equation provided by Granier (1987) significantly underestimated tree water use when compared with other published estimates at the Aracruz site (Almeida et al., 2007). Consequently, we developed a specific calibration curve for the clones and probes used in this study. Four *Eucalyptus grandis* × *urophylla* trees (5 years old and of similar size as our sample trees, Veracel clone # 43) were harvested at a BEPP site in Piracicaba Brazil, near the University of Sao Paulo campus (2 km far from the lab). Sections 0.36 m in length at tree-DBH were removed and immediately immersed in water and transported to the lab. Trunk segments were re-cut underwater and connected to a pressurized hydraulic instrument designed for testing sap flow sensors (Fernandez et al., 2001). Low to high flow rates per unit sapwood area through the stem were achieved by varying the pressure applied and forcing distilled, filtered water through the stem segment. Flow rates through the stem were measured gravimetrically using a digital scale connected to a data logger. Two thermal dissipation probes were inserted on opposite sides of the trunk and differences in temperature between the upstream and downstream probes were recorded (as described above). We calculated the dimensionless coefficient K as given in (Granier, 1987) and fit a power function to the relationship between K and actual stem flow (Fig. 1):

$$\nu = 304.46 \times K^{1.606} \quad (1)$$

2.5. Gap filling

Missing data is a common problem when conducting sap flow studies over long periods of time. There were a total of 36 missing days at the Aracruz site and 2 days missing at Veracel. Other studies have used linear regression to develop models that predict water movement in trees from climate data, but because climate data has an inherent lack of independence, results from gap filling using this approach may be less robust than others (Ford et al., 2005). Here, we utilize a trigonometric regression approach that accounts for lack of independence by adding trigonometric

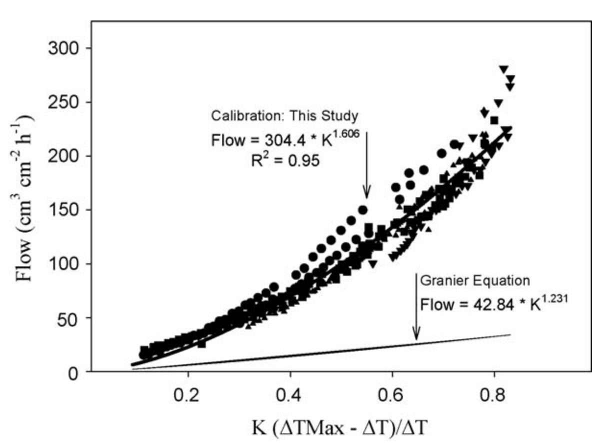

Fig. 1. Species and probe specific calibration curve for *Eucalyptus grandis* × *urophylla* clones used to calculate sap flux density at the Aracruz and Veracel sites ($n = 4$).

parameters to the model including assumptions that data points are equally spaced and the length of the period is known (Graybil, 1976). We estimated hourly v for missing days by fitting a trigonometric model to measured sap flux densities and climate data collected on site. Photosynthetically active radiation (PAR) and vapor pressure deficit (VPD were the best predictors of v, accounting for approximately 92% of the observed variability ($R^2 = 0.92$, data not shown).

2.6. Transpiration and canopy conductance

Replicate plots in our study received the same amount of resources, were equally spaced and planted on the same date resulting in homogenous stands. Consequently, we assumed sap flux per unit sapwood area did not differ between plots in the same block of the same treatment and measured average v in a single plot for each treatment. Because statistical tests revealed no significant difference in v between treatments at either site ($p > 0.05$, Fig. 4), we calculated an average sap flux density based on sample trees from both treatments ($n = 40$ at Aracruz and $n = 20$ at Veracel) and estimated canopy transpiration (E_c) in replicate plots as the product of average v and sapwood area derived from quarterly diameter measurements and our allometric equations (Fig. 2). Transpiration per unit leaf area (E_l) was determined in a similar way and estimated as the quotient of E_c and monthly LAI measurements.

We estimated canopy conductance (G_t, mmol m^{-2} leaf area s^{-1}) under high light (>900 μmol m^{-2} s^{-1}) as:

$$G_t = \frac{E_l}{D} \tag{2}$$

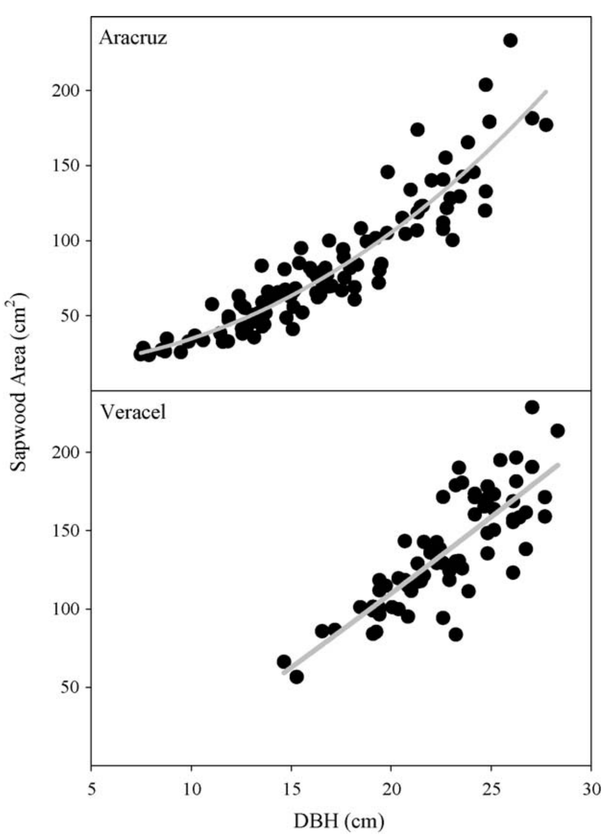

Fig. 2. Sapwood area (SWA) versus diameter at breast height (DBH) for Aracruz and Veracel study sites. Both models were power functions ($y = B_o + \alpha x^{B_1}$) with the following parameters: $B_o = 14.39$, $\alpha = 0.14$, $B_1 = 2.16$; and $B_o = -61.97$, $\alpha = 6.01$ $B_1 = 1.12$ for the Aracruz and Veracel sites respectively. All parameters were significant as indicated by 95% boot strapped confidence intervals.

where D is air saturation deficit in partial pressure units (kPa/kPa) (Whitehead et al., 1996) and assumed a well coupled canopy at both sites based on an analysis of changes in v with wind speed (Hubbard et al., 2004).

2.7. Growth measurements and water use efficiency

Growth measurements began shortly after plantation establishment (December, 2001 and March 2002 for Aracruz and Veracel respectively). Diameter at breast height was measured quarterly on all 36 trees in each replicate treatment until the end of our study. Quarterly water use efficiency was calculated as the total monthly carbon increment (50% of stem biomass) (Stape et al., 2010) for each replicate plot divided by the total amount of monthly water use.

2.8. Statistics

We used a repeated measures analysis (GLM, SPSS Inc.) to examine the effects of irrigation on water use and water use efficiency. Individual measurement trees served as our experimental unit to assess differences in v ($n = 20$ and $n = 10$ for Aracruz and Veracel sites respectively) and plot level estimates were used to detect differences in E_c, E_l and water use efficiency ($n = 3$ and $n = 4$ for Aracruz and Veracel respectively). Differences between treatments in the response of light saturated G_t with air saturation deficit were evaluated using analysis of covariance.

3. Results

The standard Granier calibration significantly underestimated sap flow for the probes and clones used in this study (Fig. 1). Flow rates calculated with the Granier equation averaged approximately five-fold lower than our calibration. Other studies have found

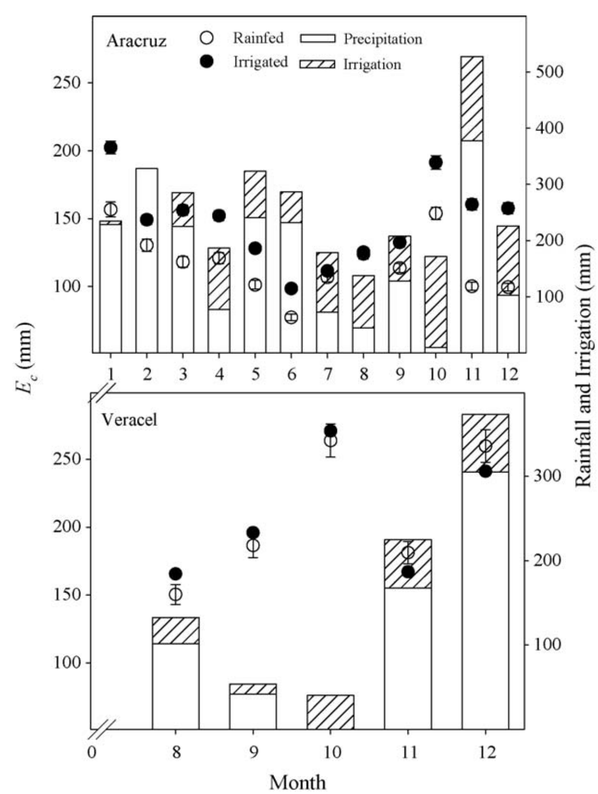

Fig. 3. Average monthly transpiration E_c, rainfall and irrigation at the Aracruz and Veracel sites. Error bars represent the variation between plots (Aracruz $n = 3$, Veracel $n = 4$).

significant departures from Granier's original equation (Taneda and Sperry, 2008; Reis et al., 2006; Lundblad et al., 2001) and together with this study reinforce Smith and Allen's (1996) recommendation that individual calibrations be performed for species not included in Granier's (1987) original study.

Annual transpiration at Aracruz was lower ($p < .01$) in rainfed (1394 mm) versus irrigated (1779 mm) treatments (Fig. 3). Transpiration accounted for approximately 67% of annual precipitation in rainfed treatments and approximately 58% of precipitation plus irrigation in the irrigated treatments (Fig. 3). Monthly transpiration averaged 116.1 mm and 148.2 mm in irrigated and rainfed treatments respectively. Transpiration rates in rainfed and irrigated treatments were highest in January (156 mm and 201 mm respectively) and the lowest monthly transpiration rates were observed in June, averaging 77 mm in rainfed treatments and 98 mm in irrigated treatments.

Similar to the Aracruz site, annual transpiration was significantly higher ($p = 0.014$) in the irrigated treatments at Veracel. Monthly transpiration at Veracel averaged 195 mm in rainfed treatments and 220 mm in irrigated treatments (Fig. 3) with the highest values occurring in October for both treatments. During the months of September and October, transpiration far exceeded precipitation and irrigation inputs suggesting trees in both treatments took advantage of stored soil water over this period.

Irrigation did not influence sap flux density (ν) ($p = 0.77$) at the Aracruz site. Monthly ν averaged 27.2 g cm^{-2} h^{-1} in rainfed treatments and 26.7 g cm^{2} h^{-1} in irrigated treatments. We found similar results at the Veracel site where monthly ν averaged 30.1 g cm^{-2} h^{-1} in rainfed treatments and 27.0 g cm^{2} h^{-1} in irrigated treatments and was not significantly different ($p = 0.43$, Fig. 4).

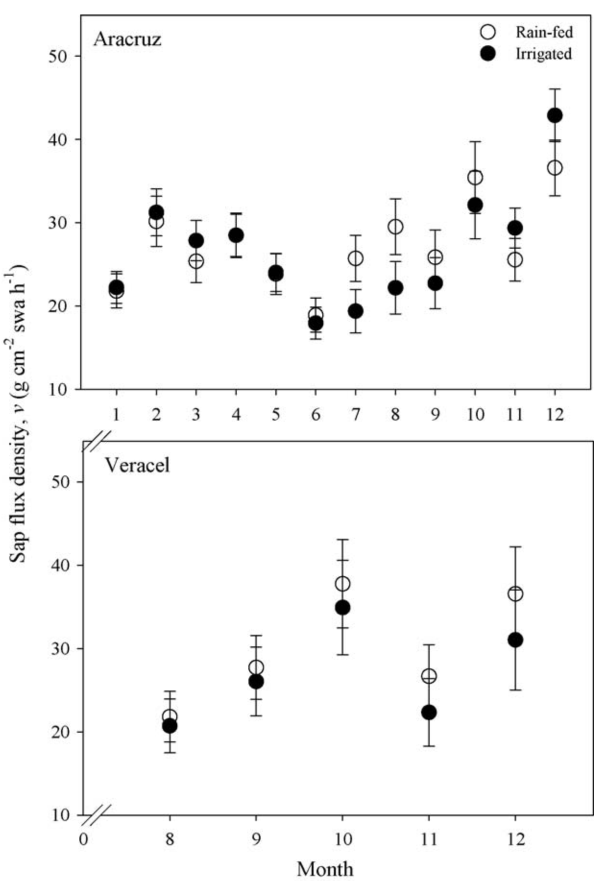

Fig. 4. Mean sap flux density at Aracruz and Veracel study sites. Sap flux density was not significantly different at the Aracruz ($p = 0.77$, $n = 20$) or the Veracel ($p = 0.43$, $n = 12$) sites. Error bars represent the variation between trees.

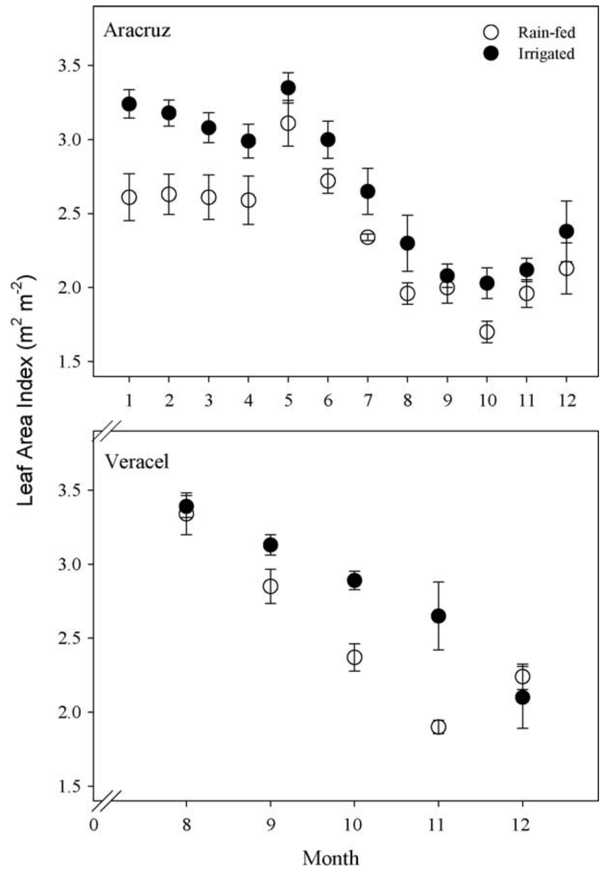

Fig. 5. Monthly LAI at the Aracruz and Veracel sites. Overall, leaf area index was significantly higher in irrigated treatments at both Aracruz ($p = 0.02$, $n = 3$) and Veracel ($p < 0.01$, $n = 4$). Error bars represent the variation between plots.

Increased transpiration rates in irrigated treatments at Aracruz were associated with higher leaf area index (LAI, m^{2} m^{-2}) in those treatments ($p = 0.02$, Fig. 5). LAI was approximately 13% higher in irrigated treatments during our study, and averaged 2.4 month^{-1} and 2.7 month^{-1} in irrigated versus rainfed treatments respectively. Increased transpiration at the Veracel site, was associated with a similar significant increase in LAI ($p = 0.01$, Fig. 5) as Aracruz. Monthly LAI in irrigated treatments at Veracel averaged 2.8 m^{2} m^{-2} compared to an LAI of 2.5 m^{2} m^{-2} in rainfed treatments. LAI at both sites was dynamic during the course of our study and declined significantly from maximum values measured. LAI at Aracruz was highest during the first 5 months (averaging 2.9 m^{2} m^{-2}) and declined to an average of 2.1 m^{2} m^{-2} from October to December. LAI decline linearly ($p < .01$) at Veracel in both treatments from an average of 3.4 m^{2} m^{-2} in August to 2.17 m^{2} m^{-2} by the end of the study.

Transpiration per unit leaf area (E_l) was significantly different between treatments at both the Aracruz and Veracel sites. E_l was approximately 10% higher ($p < 0.01$) in irrigated treatments at the Aracruz site averaging 86.8 kg m^{-2} compared to 77.4 kg m^{-2} in rainfed treatments (Fig. 6). Values were highest during October at 90.0 kg m^{-2} for rainfed treatments and 95.3 kg m^{-2} for irrigated treatments. The lowest values for rainfed and irrigated treatments occurred in June at 28.4 kg m^{-2} and 33.0 kg m^{-2} respectively. Interestingly, E_l was higher in rainfed compared to irrigated treatments at Veracel but only during October and November when differences in LAI between treatments were the highest (Fig. 5).

Light saturated G_t exhibited a typical decline with increasing saturation vapor pressure deficit at both study sites but was not

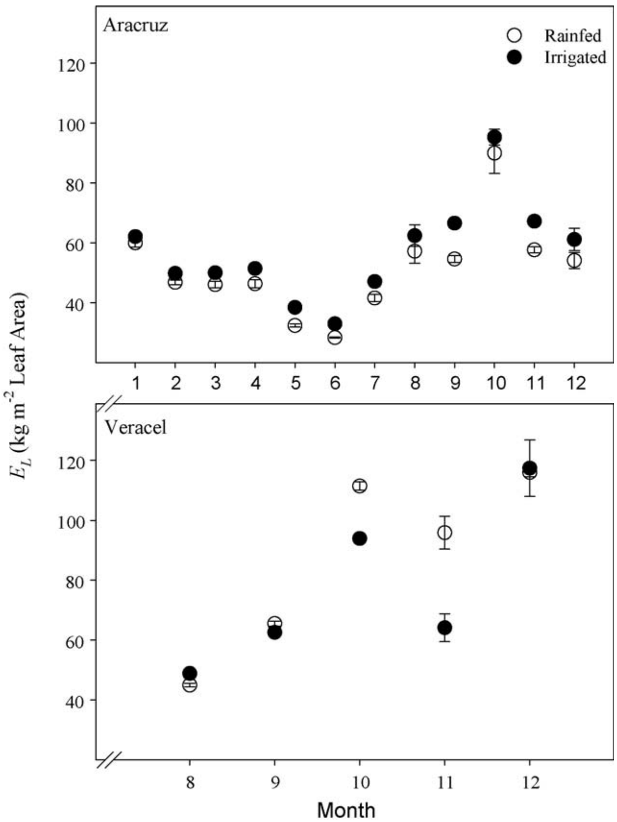

Fig. 6. Transpiration per unit leaf area (E_l) per month. E_l was significantly higher in rainfed versus irrigated treatments at Aracruz ($p < 0.01$). E_l at the Veracel was not significantly different in months 8, 9 and 12 ($p > 0.05$) but was higher in rainfed treatments during October and November ($p < 0.01$ when differences in leaf area were the largest). Error bars represent the variation between plots (Aracruz, n = 3, Veracel, n = 4).

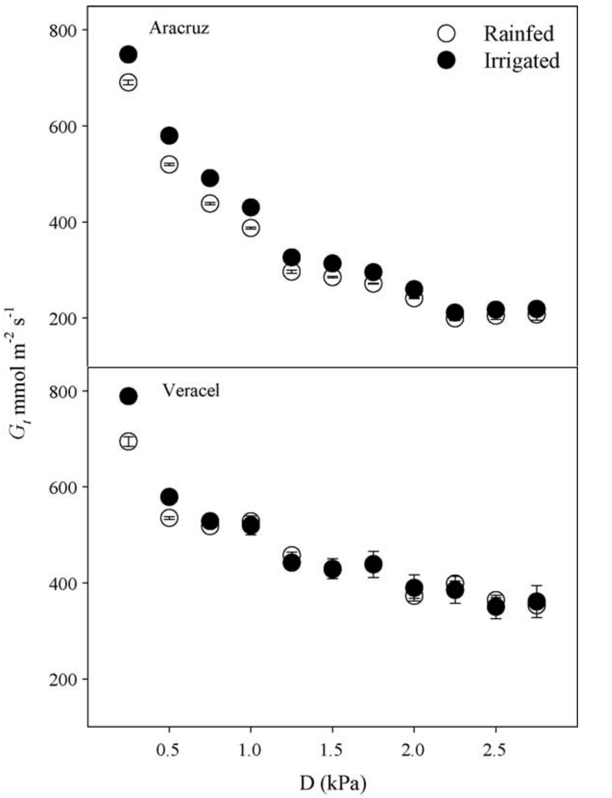

Fig. 7. Light saturated canopy conductance (G_t) response to vapor pressure deficit (D). Irrigation did not influence canopy conductance ($p > .05$) relative to rainfed treatments at either site. Error bars represent variation between plots (Aracruz, n = 3, Veracel, n = 4).

significantly different between treatments ($p > 0.05$, Fig. 7). At Aracruz, G_t declined from a high of 690 mmol m^2 s^{-1} and 740 mmol m^{-2} s^{-1} at low D in rainfed and irrigated treatments respectively to 187 mmol m^{-2} s^{-1} in rainfed and 198 mmol m^{-2} s^{-1} in irrigated treatments at high D. We found similar results at Veracel where G_t declined from a high of 694–353 mmol m^{-2} s^{-1} in rainfed and 789–361 mmol m^{-2} s^{-1} irrigated treatments.

Although irrigation caused a significant increase in above ground bole carbon increment through the majority of the BEPP

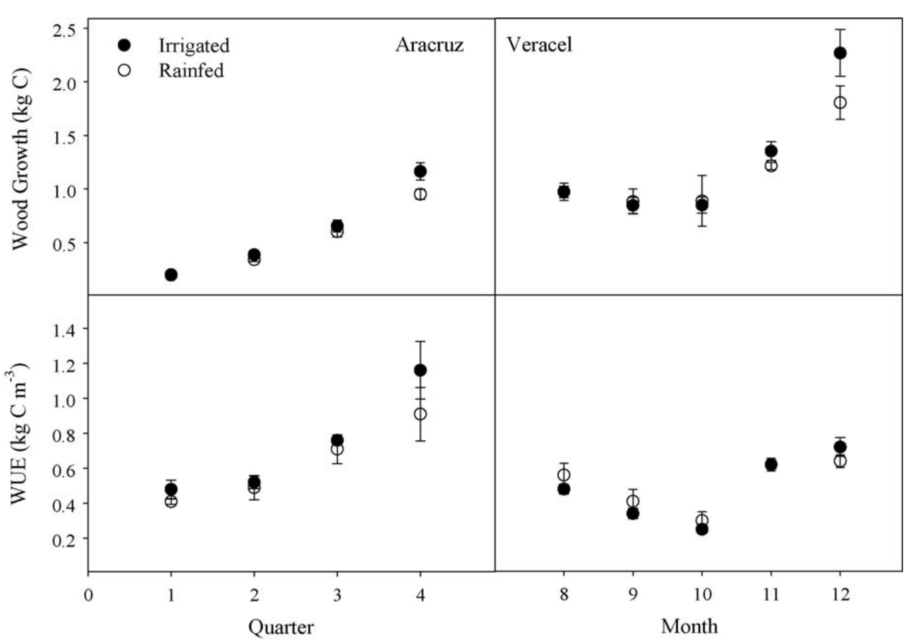

Fig. 8. Wood growth and water use efficiency at the Aracruz and Veracel sites. There was no significant difference in WUE at Aracruz (p = 0.21, n = 3) or Veracel (p = 0.45, n = 4) respectively. Error bars represent the variation between plots.

study, there was not a significant treatment difference during our measurement period (Stape et al., 2010). Likewise, water use efficiency did not differ by treatment at either site ($p = 0.21$ and $p = 0.45$) for Aracruz and Veracel respectively. Monthly water use efficiency at Aracruz averaged 0.73 kg C m^{-3} and 0.63 kg C m^{-3} in rainfed and irrigated treatments respectively. Water use efficiency at the Veracel site averaged 0.47 kg C m^{-3} in rainfed treatments and 0.51 kg C m^{-3} in irrigated treatments (Fig. 8).

4. Discussion

Irrigation led to an approximate 26% increase in annual E_c when compared to rainfed treatments at the Aracruz site (Fig. 3). Annual E_c in rainfed treatments was 1394 mm and is similar to other studies that have estimated transpiration in *Eucalyptus* trees from stands receiving similar amounts of mean annual precipitation (MAP). Dye et al. (2004) estimated annual transpiration in *Eucalyptus grandis* × *camaldulensis* clones using heat pulse sap flow sensors at two sites in South Africa (MAP ~ 1100 mm and 1390 mm) and found rates ranging from 900 mm to 1400 mm per year. Almeida et al. (2007) estimated lower annual transpiration at the Aracruz site in an experimental catchment dominated by *Eucalyptus grandis* hybrid plantations (30% of the catchment was native forest) using a water balance approach. They estimated that annual transpiration ranged from 635 mm to 1092 mm over a 6-year period. Precipitation averaged 1147 mm over the same time period and never exceeded 1507 mm y^{-1}. The percentage of precipitation removed by transpiration (77%) was similar to that found in rainfed treatments in this study (68%). We suspect higher E_c during our study is related to increased fertilization on the BEPP study plots and higher MAP during the study period.

It is also possible that our sap flow probes and calibration may have overestimated water use at Aracruz and Veracel. To address this possibility, we used a water balance model calibrated for the Aracruz plantations (Soares and Almeida, 2001) to provide an independent estimate of transpiration in the rainfed treatments at Aracruz. Annual water use as measured in this study was about 10% higher (1394 mm) than estimated by the model (1271 mm). Monthly estimates compared well ($R^2 = 0.75$) with the exception of October where modeled estimates were much lower than our sap flow measurements (43 mm compared to 152 mm respectively). We suspect that this discrepancy is attributed to access to deep soil water by these *Eucalyptus* clones that was unaccounted for in the model.

Water loss via transpiration is an inevitable consequence of carbon uptake through stomata for photosynthesis and a comparison of water use within and between the Aracruz and Veracel sites indicate higher productivity in these *Eucalyptus* plantations is associated with increased stand water use. Like Aracruz, irrigated treatments at Veracel had a positive influence on stand water use where E_c totaled 977 mm in rainfed and 1102 mm in irrigated treatments during the 5-month comparison. During the same measurement period, E_c at Aracruz totaled 600 mm and 759 mm in rainfed and irrigated treatments respectively. Above ground net primary production was similarly higher at Veracel averaging 38 Mg ha^{-1} y^{-1} versus 26 Mg ha^{-1} y^{-1} at Aracruz (Stape et al., 2010). Although our study sites are located in relatively wet regions and 2005 was an abnormally wet year, these results and other work (Florence, 1996; Stape et al., 2004) suggests that tradeoffs between increased productivity and water use should be carefully considered in dryer areas and in light of potential changes in precipitation with climate change.

Increased water use in the irrigated treatments at Aracruz and Veracel was associated with an increase in leaf area (Fig. 5). Despite a significant decline in LAI for both treatments at these two sites during the measurement period, LAI values in irrigated treatments averaged about 10% higher over the course of this study. A strong positive relationship between E_c and increased leaf area is not uncommon in *Eucalyptus* species and has been observed following increased nutrient supply (Myers et al., 1996; Hubbard et al., 2004), across precipitation gradients (Stape et al., 2004) and in plantations with differential access to ground water (Benyon et al., 2006).

The response of G_t with air saturation deficit (D) was similar between rainfed and irrigated treatments at both sites (Fig. 7). In a review of *Eucalyptus* physiology and productivity, Whitehead and Beadle (2004) indicated stomatal conductance in *Eucalyptus. grandis* was less sensitive to D than other *Eucalyptus* species (Dye and Olbrich, 1993). The relationship of G_t with D (Fig. 7) in both of our treatments indicate higher stomatal sensitivity to D than reported by Dye and Olbrich (1993) but similar to published values in the same region (Mielke et al., 1999; Soares and Almeida, 2001) however maximum light saturated G_t in this study was almost double. Marrichi (2009) also found high light saturated stomatal conductance in the Veracel and Aracruz clones a similar response g_s with D. Results from this study are consistent with the work by Oren et al. (1999) where they found species and stands with higher stomatal conductance at a reference D of 1 kPa exhibit a higher stomatal sensitivity to D.

It is unlikely that the *Eucalyptus grandis* × *urophylla* trees in either treatment experienced significant soil water deficits during the study given the large precipitation inputs (Fig. 3). Likewise, growth rates for these treatments were similar during the year of our study but large differences were more evident earlier in the rotation (Stape et al., 2004) possibly leading to a larger separation in G_t and E_l between treatments. We are planning further experiments at the Veracel site that will control soil water availability through the use of precipitation exclosures and monitor transpiration and growth during the period of maximum growth differences between treatments.

Increased water availability in irrigated treatments did not influence water use efficiency at either of our study locations (Fig. 8) although Almeida et al. (2007) showed that water use efficiency in this species varies dramatically during the rotation decaying with LAI and stand age. In addition, because there was no significant dry period during our study, it remains unclear as to the effect of irrigation on these clones during times of limited soil water availability. In support of the current study, other work suggests increased water availability may not negatively impact water use efficiency in similar *Eucalyptus* plantations. Stape et al. (2008) found irrigation increased water use efficiency approximately 28% during a 2-year study in a single *E. grandis* plantation and found a positive correlation of water use efficiency with increasing productivity and precipitation in Brazil (Stape et al., 2004). Ngugi et al. (2003) showed that three different 7-month-old *Eucalyptus* clones exhibited similar water use efficiency at high, medium and low water availability indicating water use and wood production were proportional. Water use efficiency has also been shown to increase during periods of limited soil water availability (Olbrich et al., 1993). Together these studies suggest that irrigation improvements in growth may not be associated with a decline in water use efficiency and proportional increases in growth and water use be evaluated strictly on a cost/benefit basis and the effect of increased water use on local and regional water balance. However more work is needed to examine how water use efficiency changes with stand development, water availability within a single site, across production gradients and under climate change scenarios.

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