Comparative water use in short-rotation *Eucalyptus benthamii* and *Pinus taeda* trees in the Southern United States

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ABSTRACT

Short rotation *Eucalyptus* plantations offer great potential for increasing wood-fiber production in the southern United States. *Eucalyptus* plantations can be highly productive (>35 m^3 ha^{-1} $year^{-1}$), but they may use more water than intensively managed pine (primarily *Pinus taeda* L.) plantations. This has raised concern about how expansion of *Eucalyptus* plantations will affect water resources. We compared tree water use, stem growth, and WUE (kg wood per m^3 water transpired) in adjacent nine-year-old *Eucalyptus benthamii* and *P. taeda* plantations with similar stand density and leaf area. Sap flux (F_d, $g\,cm^{-2}\,s^{-1}$) was measured continuously over one year using thermal dissipation probes. Stem biomass, stem growth, tree water use (E_t, $L\,day^{-1}$), canopy transpiration per unit leaf area (E_l, $mmol\,m^{-2}\,s^{-1}$), and canopy stomatal conductance (G_s, $mmol\,m^{-2}\,s^{-1}$) were quantified. *Eucalyptus* had higher daily F_d (196.6 $g\,cm^{-2}\,day^{-1}$) and mean daily E_t (24.6 $L\,day^{-1}$) than pine (105.8 $g\,cm^{-2}\,day^{-1}$, 15.2 $L\,day^{-1}$). *Eucalyptus* exhibited a seasonally bimodal pattern in daily E_t that did not occur in pine. Monthly E_t was 23–51% higher in *Eucalyptus* and differences between species were greatest in the spring and fall. Annual E_t was 32% higher in *Eucalyptus* (9.13 m^3 H_2O $year^{-1}$) than pine (5.79 m^3 H_2O $year^{-1}$). Annual stem biomass increment was greater in *Eucalyptus* (*Eucalyptus*: 22.9; pine: 11.8 kg $tree^{-1}$ $year^{-1}$), and *Eucalyptus* had greater WUE (*Eucalyptus*: 2.86; pine 1.72 kg biomass m^{-3} H_2O $year^{-1}$). Pine exhibited a lower seasonal minimum and higher seasonal maximum leaf area index (LAI). At low LAI, there was no significant difference between species in E_l or G_s; however, at maximum LAI, pine E_l and G_s were 46 and 43%, respectively of rates observed in *Eucalyptus*. The species differed in G_s response to vapor pressure deficit (D). At a similar reference G_s ($G_{s,ref}$ at $D = 1$ kPa), pine exhibited greater stomatal sensitivity to D. These results suggest that (1) *Eucalyptus* trees had higher sap flux and total water use than pine, (2) *Eucalyptus* had greater stem growth and WUE, and (3) species differences in water use were driven primarily by differences in E_l and G_s.

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1. Introduction

In the Southern US, plantation forests are dominated by loblolly (*Pinus taeda* L.) and slash (*P. elliottii* Engalm) pine (16 million ha, Fox et al., 2007). Loblolly pine plantation silviculture, genetics, and forest operations are highly advanced making it a prime candidate for commercial bioenergy feedstock production (Kline and Coleman, 2010). However, frost tolerant, fast-growing *Eucalyptus* species are now being considered as an alternative short-rotation plantation species for pulp and feedstocks for bioenergy and bioproducts (Hinchee et al., 2009; Gonzalez et al., 2011; Dougherty and Wright, 2012,) and could potentially replace pine on some sites (Stanturf et al., 2013) particularly at lower latitudes.

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Eucalyptus plantations can be highly productive (>35 m^3 ha^{-1} year^{-1}) (Albaugh et al., 2013) compared to conventionally grown pine (25–27 m^3 ha^{-1} yr^{-1}) (Fox et al., 2007). Eucalypts have other advantages including short rotation length (6–8 years), potential for planting on marginal lands, ability to coppice producing multiple crops from a single planting, high wood bulk density, and excellent wood and fiber properties (Dougherty and Wright, 2012). Susceptibility to cold damage has limited commercial production of *Eucalyptus* in the Southern US (Vance et al., 2014). However, identification of frost tolerant species and hybrids along with improved silviculture protocols may make it possible to grow commercially viable plantations in USDA Plant Hardiness Zones 8b and higher (annual minimum temperature > 9.4 °C (USDA, 2012). For example, *Eucalyptus benthamii* has shown superior growth (Hall, 2015) and can tolerate temperatures to -12 °C (Johnsen, *personal communication*) making this species suitable for much of the Gulf and Atlantic Coastal Plains in the Southern US.

The potential for widespread cultivation of *Eucalyptus* in the Southern US has presented several environmental considerations including unknown impact on biodiversity, susceptibility to fire, invasiveness (Callaham et al., 2013; Lorentz and Minogue, 2015), and water use (Stanturf et al., 2013). *Eucalyptus* culture is often linked to high water use relative to other species (Scott, 2005; Hubbard et al., 2010; Albaugh et al., 2013) and is controversial in some parts of the world because they often use more water than the vegetation they replace (Farley et al., 2005; Ferraz et al., 2013) and can reduce off-site water yield (Calder, 2002). Productivity and water use are tightly coupled and morphological and physiological traits such as high stomatal conductance, drought tolerance, evergreen leaves, and deep rooting (Whitehead and Beadle, 2004) contribute to *Eucalyptus* plantations having some of the highest evapotranspiration rates of tree species (Dye, 2013; Farley et al., 2005; Hubbard et al., 2010). Potential high water use and rapid growth coupled with the region's high potential evapotranspiration (PET) have important implications for the sustainable short-rotation production of *Eucalyptus* in the Southern US (Vose et al., 2015).

Intensively managed forest plantations generally use more water than less intensively managed or native forests (Cannell, 1999; Jackson et al., 2005); however, it is unknown if *Eucalyptus* plantations will use more water than intensively managed pine (*P. taeda, P. elliotii*) grown in the Southern US. Studies comparing water use between *Eucalyptus* and other species are rare (although see Benyon and Doody, 2015). Farley et al. (2005) showed that converting grasslands to *Eucalyptus* plantations reduced runoff 25% more than converting grassland to pine indicating a higher rate of water use in *Eucalyptus*. Myers et al. (1996) found after several years of irrigation, that 3-year-old *E. grandis* plantations had 42% greater standing volume and use 22% more water than *P. radiata*. Similarly, in France, Moreaux et al. (2012) found that hybrid *Eucalyptus* (*E. gunni x dalrympleana)* plantations had 25% higher evapotranspiration compared to native maritime pine (*P. pinaster*), but *Eucalyptus* had 1.6× greater water use efficiency (WUE: biomass growth per unit water transpired). In both of the above studies, the authors concluded that species differences in water use were a function of growth rate and stage of stand development and not to inherent differences in species physiology. Water use efficiency relates productivity and water consumption and is a useful metric to compare species water use and understand the relationship between water use, stand growth, and development. *Eucalyptus* plantations generally have high WUE (Stape et al., 2004) and fast growing *Eucalyptus* trees are thought to use water more efficiently than slower growing trees (Otto et al., 2014); however, it is unknown if *Eucalyptus* has greater WUE than pine, but evidence from overseas studies suggest a higher WUE for *Eucalyptus* (White et al., 2009). Understanding the physical and biological factors that regulate water use and quantifying species differences in water use and WUE are important for evaluating the hydrological behavior of short-rotation forest systems and implications for water resources.

Water consumption of short-rotation *Eucalyptus* plantations needs to be quantified in order to develop management and silvicultural practices that maximize productivity and WUE without compromising water resources and for evaluating the impact on water resources of replacing pine with *Eucalyptus*. Our objective was to compare tree water use and WUE over one year in adjacent nine-year-old stands of *E. benthamii* and *P. taeda* plantations growing in the Coastal Plain of South Carolina. We hypothesized that *Eucalyptus* would have higher sap flux and tree water use, but because of greater growth and efficient stomatal regulation, *Eucalyptus* trees would have greater WUE.

2. Methods

2.1. Study site

The study site was located near Ravenel, SC (32°45′N80°14′W). The climate is warm and humid. Average January and July temperatures are 8.0 and 27.3 °C, respectively (1981–2010; NOAA Climate Data for Charleston, SC). Annual rainfall is 1345 mm with 37% of this occurring during summer (June–August). Potential evapotranspiration (PET) generally is less than annual precipitation, although extended droughts during the growing season are common. The soils are a fine-loamy, mixed, active, thermic Typic Endoaqualfs (Yonges series) and are poorly drained with a high water table. Tree sap flux and growth were measured in adjacent stands of nine-year-old *E. benthamii* and *P. taeda*. Stands were separated by a 10 m wide access road. The *E. benthamii* stand was a provenance test planted in 2004. Seedlings were flat planted at 3 × 3 m spacing (1080 trees ha^{-1}). The *Eucalyptus* stand was devoid of understory vegetation. The pine stand was planted with mass control pollinated seedlings on beds at 1.8 × 4.3 m spacing (1280 trees ha^{-1}). The understory in the pine was mechanically removed in a 650 m^2 area (84 trees) prior to the experiment. Regrowth of the understory was minimal during the study. Twelve trees of each species with diameters within one standard deviation of the stand mean with no missing adjacent trees were selected for sap flux measurement (Table 1). Plot areas were 108 and 94 m^2 for the *Eucalyptus* and pine, respectively.

2.2. Environmental monitoring

Air temperature, relative humidity (Vaisala HMP-60, Campbell Scientific, Logan, Utah), photosynthetically active radiation (PAR) (LI-190s, Licor, Lincoln, NE, USA), and precipitation were measured in an open field adjacent to the study site. Precipitation and PAR were also measured in the understory. Vapor pressure deficit (*D*, kPa) was calculated from relative humidity and air temperature (Jones, 1986). Soil volumetric water content (VCW, m^3 m^{-3}) was measured continuously at one location in each plot using a multiple annular capacitance sensor (Sentek PTY LTD, Adelaide, Australia) placed at 30 cm.

2.3. Biometric measurements and tree biomass

Stem diameter (cm) at 1.3 m (dbh) was measured bimonthly or monthly. Daily changes in diameter were estimated by interpolation and were used to estimate sapwood area (A_s). Sapwood thickness in *E. benthamii* was measured visually from a clearly defined color change at the boundary between sapwood and heartwood (2.99 ± 27 cm, n = 10). Sapwood area was derived from over bark diameter using an exponential expression, where A_S (cm^2)

Table 1
Plot characteristics of tree ($n = 12$) height, diameter at breast height (DBH), diameter growth, stem biomass and biomass increment, sapwood area (A_s), tree leaf area (A_l), ratio of sapwood to leaf area (A_s/A_l), and ratio of sapwood to the ground area occupied by each tree (A_s/A_g) for nine-year-old *E. benthamii* and *P. taeda* trees. Values are LSMEANs and standard error (SE). Plot-level leaf area index (LAI$_P$), tree density, and basal area (BA) are also given.

Variable	*E. benthamii*[1]	*P.taeda*	SE	*P-value*
Height (m)	19.0[a]	13.3[b]	0.9	0.001
DBH (cm)	16.6[a]	14.5[a]	0.9	0.126
Diameter growth (cm^2)	1.79[a]	1.68[a]	0.18	0.644
Stem biomass (kg tree^{-1})	114.9[a]	44.7[b]	10.8	<0.001
Stem increment (kg tree^{-1} yr^{-1})	22.9[a]	11.8[b]	2.9	0.013
A_s (cm^2)	113.0[a]	125.6[a]	10.6	0.421
A_l (m^2)[2]	24.3[a]	39.7[a]	4.0	0.020
A_s/A_l (cm^2 m^{-2})	5.74[a]	3.18[b]	0.42	0.001
A_s/A_g (cm^2 m^{-2})	13.3[a]	16.1[b]	0.4	<0.001
LAI$_P$ (February)	2.40	2.03	NA[3]	NA
LAI$_P$ (September)	2.92	3.71	NA	NA
Density (trees ha^{-1})	1084	1280	NA	NA
BA (m^2 ha^{-1})	24.9	21.6	NA	NA

[1] Superscript letters denote significant differences across rows at $\alpha = 0.05$.
[2] Tree leaf area for pine is total (all-sided) leaf area.
[3] Not applicable.

$= -33.245 + 6.087 * \text{diameter}^{1.129}$ ($R^2 = 0.91$). In *P. taeda*, all of the xylem was considered hydro-active as heartwood does not develop until 15–20 years (Schultz, 1997).

Continuous measurement of stem diameter was made using custom-made automated dendrometer bands. Bands consisted of a metal tape, spring, and a potentiometer (*Robert Teskey, personal communication*). Bands were installed in mid-April on all of the trees. However, because of equipment failure or inconsistent signals from the potentiometers only nine *Eucalyptus* and ten pine trees provided useful data. Therefore, data from the automated bands are used only to describe seasonal patterns of stem growth.

Stem and foliage biomass was estimated from stand-specific allometric equations. Equations for *Eucalyptus* are given in Hall (2015). For the pine, six trees were harvested at the end of the study and partitioned into stem, foliage and branches. Stem biomass was estimated as $\ln(\text{stem biomass}) = -1.8606 + 2.1065 * \ln(\text{dbh})$ ($R^2 = 0.93$, MSE = 0.1040, $P = 0.002$) and tree foliage biomass as $\ln(\text{foliage biomass}) = -7.5544 + 3.2364 * \ln(\text{dbh})$ ($R^2 = 0.98$, MSE = 0.0799, $P < 0.001$). Annual stem biomass increment was estimated as the difference between biomass at the beginning and end of the study.

Plot-level leaf area index (LAI$_P$) was measured in February and September using a LAI-2000 Plant Canopy Analyzer (Licor Inc, Lincoln, NE, USA) (Table 1). These months correspond to the annual minimum and maximum LAI for *P. taeda* (Albaugh et al., 1998). The seasonal pattern of pine LAI$_P$ was simulated following Sampson et al. (2003) (Fig. 1). No LAI$_P$ data were available for *E. benthamii* in the Southern US. However, in the southern hemisphere, the LAI of *Eucalyptus* sp. plantations under non-limiting soil moisture are typically at an annual minimum in early spring and maximum in late summer (Whitehead and Beadle, 2004). We assumed that *Eucalyptus* LAI$_P$ in February and September measurements represented the seasonal minimum and maximum and a linear increase in LAI$_P$ (White et al., 1998) from March through September. Tree-level leaf area index (LAI$_T$) was estimated as the quotient of tree leaf area and the ground area occupied by each tree in the plot. Ground area for each tree (A_g) was the proportion of plot area occupied by each tree adjusted for tree size (i.e. tree cross sectional stem area at DBH divided by the plot area: *Euclayptus*: 108 m^2; pine: 94 m^2). Tree leaf area in February was determined from tree foliage biomass and specific leaf area (pine: 50 cm^2 g^{-1}; Vose and Allen, 1988). As no specific leaf area data was available for mature *E. benthamii*, we assumed a value of 60 cm^2 g^{-1} typical for plantation *Euclaytus sp* (Whitehead and Beadle, 2004). Mean tree LAI$_T$ in February was 2.48 ± 0.15 SE and
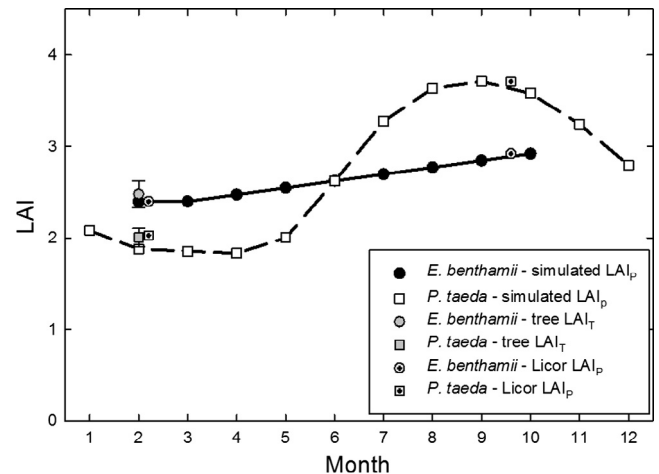
Fig. 1. Monthly simulated plot leaf area index (LAI$_P$) compared to measured LAI$_P$ and estimated individual tree LAI (LAI$_T$).

2.01 ± 0.08 SE for *Eucalytpus* and pine, respectively, which compared well to the measured LAI$_P$ (Fig. 1). LAI$_T$ for other times of the year was adjusted based on the seasonal dynamics of LAI$_P$.

2.4. Sap flux density measurements

Sap flux density (F_d) was measured using custom-made 20 mm thermal dissipation probes (TDP) similar to Granier (1985). Each tree was instrumented using two probes per tree installed in the outer 20 mm of sapwood on an east and west azimuth between 1.2 and 1.6 m above the soil surface. Three or four trees in each stand had an additional 20 mm probe installed at the 20–40 mm depth perpendicular to the outer probes to measure the sap flux radial profile (Phillips et al., 1996). Outer TDPs were installed in January and inner probes installed in July and August. Probes were shielded from radiation heating using aluminum pans. Voltage signals from the probes were queried every 15 s and the 30 min average recorded using a data logger (CR-1000, Campbell Scientific). Sap flux density (F_d, g m^{-2} s^{-1}) was calculated using the standard equation (Granier, 1985):

$$F_d = 119 * ((\Delta T_{max} - \Delta T)/\Delta T)^{1.231}, \tag{1}$$

where ΔT is the temperature difference between heated and unheated probe and ΔT_{max} is the ΔT under no flow conditions

($F_d = 0$) usually occurring at night. *Eucalyptus* and pine are known to have significant nocturnal F_d at high D (Oren et al., 1999; Phillips et al., 2010). ΔT_{max} was calculated using a program that accounted for the effects of nighttime F_d on the baseline signal (Baseliner, Duke University, Oishi et al., 2008). Conditions for zero nighttime flow were met when average $D < 0.05$ kPa for at least two hours.

Sap flux density measured at 20–40 mm xylem depth was lower than in the outer xylem (0–20 mm), and the relationship between inner and outer xylem was linear (Fig. 2). In *Eucalyptus*, F_d at 20–40 mm was $0.09 * F_d$ (i.e. average slope of all trees) of the outer 0–20 mm. Sapwood thickness was 30.3, 23.6, and 23.6 mm in trees 2, 6, and 9, respectively indicating that 50–82% of the inner probe was in contact with non-conducting xylem, which can result in an underestimate of F_d (Clearwater et al., 1999). Inner xylem F_d corrected for the proportion of the probe in non-conducting xylem (Clearwater et al., 1999) was on average $0.16 * F_d$ in the outer xylem. This ratio was use to estimate F_d for xylem >20 mm. In pine, F_d at 20–40 mm was $0.58 * F_d$ of the outer sapwood similar to that reported by Phillips et al. (1996) for 12 year-old trees. To estimate F_d of deeper xylem (>40 mm), a three parameter Gaussian function was used to calculate the radial distribution of F_d (Ford et al., 2004):

$$F(x) = \alpha * \exp((-0.5((x - x_o)/\beta)^2) \qquad (2)$$

where x is xylem depth from the cambium, α is maximum F_d, and x_o is depth of maximum F_d (in this case, 0–20 mm). The β parameter describes the radial profile and is inversely related to the rate of decrease in F_d with depth and was estimated from the ratio of F_d (20–40 mm)/F_d (0–20 mm). An average F_d was computed as the sum of F_d for each 20 cm segment weighted by the relative proportion of total sapwood at that depth (Hatton et al., 1990).
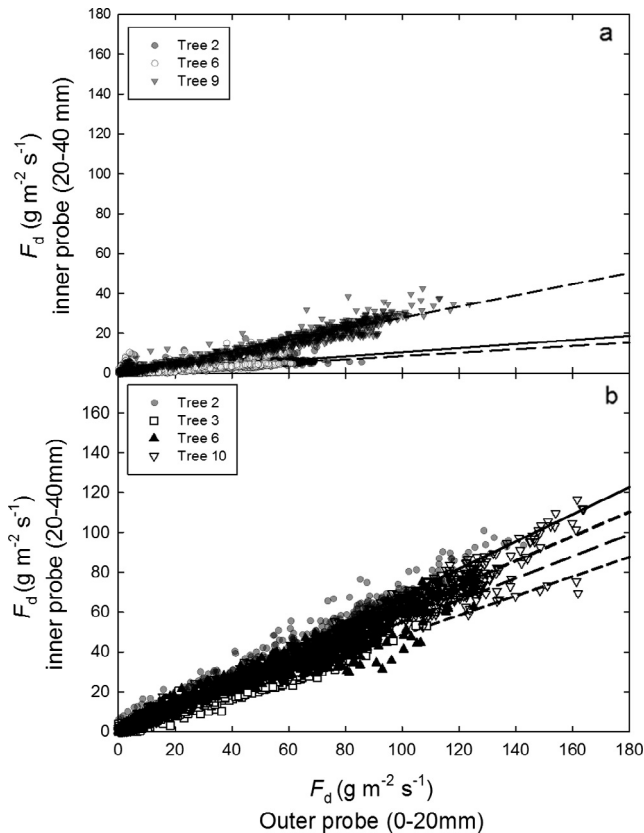

Fig. 2. The relationship between F_d in the inner (20–40 mm) and the outer (0–20 mm) xylem in *Eucalyptus* (a) and pine (b) measured between day of year 230 and 304. Each data point is the hourly average F_d.

2.5. Calculation of tree transpiration and canopy conductance

Tree water use or transpiration (E_t) was calculated for each 30 min period as the product of F_d and A_s and summed to daily (L day^{-1}), monthly, or annual (m^3 H$_2$O month^{-1} or year^{-1}) E_t. Similarly, tree transpiration on a ground area basis ($E_{t,g}$, mm day^{-1}) was calculated as the product of F_d and A_s/A_g, where A_g is the proportion of the plot area occupied by the tree (Section 2.4). There were two days of missing data from the pine stand and 17 days missing from the *Eucalyptus* stand that occurred between day of year (DOY) 208 and 224. Daily E_t for missing days was estimated for each tree using a quadratic equation and D based on E_t measured five days before and after missing data. D explained 88–94% of the variation in daily E_t for both species.

Transpiration per unit leaf area (E_l, mmol m^{-2} s^{-1}) was estimated by dividing E_t by LAI$_T$. Canopy stomatal conductance (G_s, mmol m^{-2} leaf area s^{-1}) was calculated from E_l and D as:

$$G_s = (\lambda * E_l * \gamma)/(\rho * c_p * D) \qquad (3)$$

where λ is the latent heat of vaporization of water (2465 J g^{-1}), γ is the psychometric constant (65.5 Pa K^{-1}), ρ is the density of air (1225 g m^{-3}), c_p is the specific heat of air (1.01 J g^{-1} K^{-1}). Eq. (3) assumes a high boundary layer conductance relative to G_s. We followed the approach of Oren et al. (1999) to analyze the sensitivity of G_s to D. Hourly G_s were fitted to the model:

$$G_s = G_{s,ref} * -m \ln D \qquad (4)$$

where $G_{s,ref}$ is reference G_s at $D = 1$ kPa and $-m$ is the slope or sensitivity to D ($-dG_s/d\ln D$). Hourly diurnal values of G_s where PAR > 1200 µmol m^{-2} s^{-1} (Samuelson and Stokes, 2006) and $D > 0.75$ kPa were used to minimize potential constraints on G_s (Ewers and Oren, 2000).

2.6. Statistical analysis

Analysis of variance was used to analyze species difference in stand characteristics (height, diameter, A_s, LAI$_T$, biomass, and growth increment), E_t, and WUE. Variables were transformed as appropriate to meet the assumptions of normality. One pine tree gave inconsistent F_d measurements and was dropped from the analysis of water use. The linear model for the analysis was

$$Y_{ij} = \mu + S_i + T_{j(i)} + \varepsilon_{ij} \qquad (5)$$

where Y_{ij} is the response of the jth tree ($j = 1, ..., 11$ or 12) in the ith species ($i = 1, 2$), μ is the population mean, S_i the effect of species, $T_{j(i)}$ is the effect of tree nested within species, and ε_{ij} is the error term. Species and tree were considered fixed and random effects, respectively. Repeated measures were used to analyze time series data (PROC MIXED) using a first order autoregressive covariance structure. Species differences in stand attributes, E_t, and WUE were determined with LSMEANs statement using Tukey's adjustment. There are important limitations to the experimental design and analyses. In Eq. (5), the individual tree was considered the experimental unit ($n = 12$); however, this is not true replication as the trees were spatially segregated into a single plot. The confounding of species and plot precluded testing for species differences, thus statistical test are subject to an inflated probability of a Type I error. However, we suggest that the confounding between species and plot is small as the plots were close in space, on the same soil type, had similar topography, and experience similar environmental conditions. Nevertheless, inferences apply only to these two plots and extrapolation to a larger population should be made with caution.

Non-linear relationships between G_s and D were analyzed using PROC NLIN. Species and season differences in regression coefficients for Eq. (4) and the proportionality of $-m$ to $G_{s,ref}$ were tested

using full and reduced models (PROC MIXED) (Zarnoch, 2009). Contrast statements were used to test for species and season effects on parameter estimates. All analyses were done in SAS (version 9.4, SAS Institute, Cary, North Carolina).

2.7. TDP calibration

Several studies have shown that the standard equation (Eq. (1)) can under or overestimate sap flux (Steppe et al., 2010; Hultine et al., 2010; Bush et al., 2010; Sun et al., 2012). Lu et al. (2004) suggested that the original calibration should be used with caution as it could vary with tree species, wood anatomy and thermal properties, and with differences in probe design and construction. We compared potometric estimates of sap flux density ($F_{d,p}$) to that estimated using the original calibration in large diameter (10–18 cm dbh) field grown trees. Whole trees were used as potometers (Roberts, 1977; Gutiérrez and Santiago, 2006; Uddling et al., 2009; Sun et al., 2012) under ambient field conditions. TDP calibrations were performed on three four-year-old E. benthamii, three nine-year-old, and two eleven-year-old P. taeda trees. Measurements were made on warm sunny days in June and July (one tree per day). On the afternoon prior to calibration, two TDP were inserted radially in the outer 20 mm of xylem on opposite sides of the tree in an east-west orientation and 50–150 cm above ground level. The Eucalyptus had shallow sapwood depth (25–32 mm), so only the outer 20 mm of xylem was measured. The pine had much deeper sapwood, so two additional probes were inserted 10 cm above and perpendicular to the outer probes at 20–40 mm to measure changes in F_d with sapwood depth. The outer 20 mm probe covered 62–80% of sapwood in Eucalyptus and the outer and inner probes together covered 49–84% of the sapwood in pine. A sapwood area average of $F_{d,g}$ was calculated based on the sapwood depth where $F_{d,g}$ for xylem in Eucalyptus > 20 mm and in pine > 40 mm was estimated as described in Section 2.4. Trees were cut in the morning before sunrise when transpiration was low to minimize xylem embolism at the cut surface. In order to move the tree after cutting and to secure the stem during measurement, the trunks were strapped to the articulating arm of a soil excavator or backhoe. Tree stems were cut diagonally near ground level with a chainsaw and cut ends immediately submerged in a 19-L reservoir filled with water. The base of the stem and reservoir were covered with insulation to minimize evaporation. Volumetric water uptake was measured every 30 min for the next 5–8 h. Potometer sap flux density ($F_{d,p}$, g m^{-2} s^{-1}) was calculated as the quotient of water uptake and sapwood area.

3. Results

3.1. TDP calibration

At mid-day (1100–1300 h), Eucalyptus used 3.5–4.6 L 30 min^{-1} compared to 0.25–3.0 L 30 min^{-1} for pine. Cumulative water uptake from 0800 to 1300 h ranged from 27.6 to 40.9 L tree^{-1} in Eucalyptus compared to 3.5 to 17.8 L tree^{-1} in pine (Fig. 3a). Eucalyptus also had higher water use per unit sapwood area (Eucalyptus: 0.48 ± 0.03; pine: 0.09 ± 0.02 L cm^{-2} five hours^{-1}). In pine, potometer measurements were 87% of estimated sap flow using the standard equation; however, this difference was not significant ($t = 0.48$, $n = 5$, $P = 0.649$). Potometer measurements of water use in Eucalyptus was 2.6-fold greater than estimated with the standard equation ($t = -9.36$, $n = 3$, $P < 0.001$). In pine, sap flux estimated with the Granier equation ($F_{d,g}$) was linearly correlated with sap flux measured with the potometer ($F_{d,p}$) ($R^2 = 0.86$) and the slope was not significantly different from 1 ($P > 0.05$) (Fig. 3b). In Eucalyptus, $F_{d,g}$ severely underestimated $F_{d,p}$. The nonlinear model
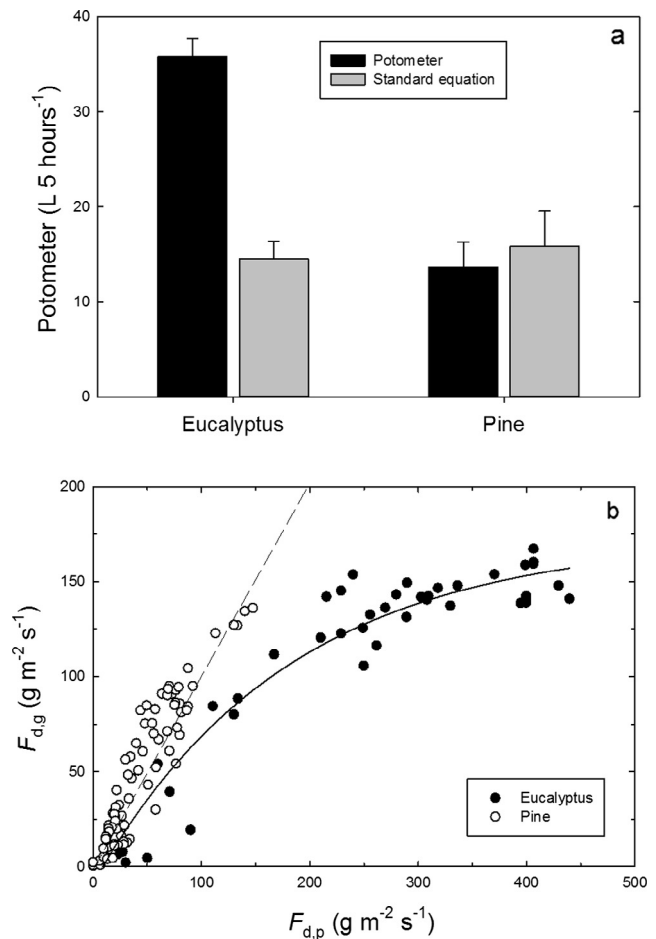
Fig. 3. (a) Mean cumulative water use over a five-hour period (0800–1300 h) measured with whole-tree potometers compared to estimated cumulative water uptake using the standard equation established by Granier (1985) ($F_{d,g} = 119x^{1.231}$). Values are means ± standard error for pine ($n = 5$) and Eucalyptus ($n = 3$). (b) Relationship between sap flux density estimated with standard equation ($F_{d,g}$) and measured with the whole-tree potometer ($F_{d,p}$). The solid line is the nonlinear regression of the form $y = 157.8(1 - e^{-0.0048x})$ ($R^2 = 0.95$). The dashed line is the 1:1 line.

($y = a*(1 - e^{-bx})$) resulted in the best fit (a = 157.8; b = 0.0048; $R^2 = 0.95$) between $F_{d,g}$ and $F_{d,p}$. This model was used to adjust F_d for Eucalyptus in the subsequent analyses.

3.2. Environmental and stand characteristics

Mean and maximum daily temperatures were typical of the 30-year average; however, there were several freezing events between November 2013 and January 2014 where daily minimum temperatures fell below -3 °C (Fig. 4a). Annual rainfall was 1630 mm, 19% greater than the 30-year average (1328 mm) with 56% of the total occurring between June and August (DOY 153-244) (Fig. 4b). Daily mean vapor pressure deficit (D) was low rarely exceeding 1 kPa, although maximum D often exceeded 2.0 kPa (Fig. 4c). There was high temporal variation in VWC (Fig. 4d). Volumetric water content at 30 cm ranged between 0.07 and 0.31 and was above 0.15 for much of the early to mid-growing season (DOY 60-240) except for a brief period in late May when VWC declined to close to 0.10. The seasonal pattern of VWC was similar between stands; however, VWC was more variable in Eucalyptus.

At the beginning of the study, Eucalyptus trees were significantly taller than pine and larger in diameter, although, diameter differences were not significant (Table 1). Ecualyptus stem biomass
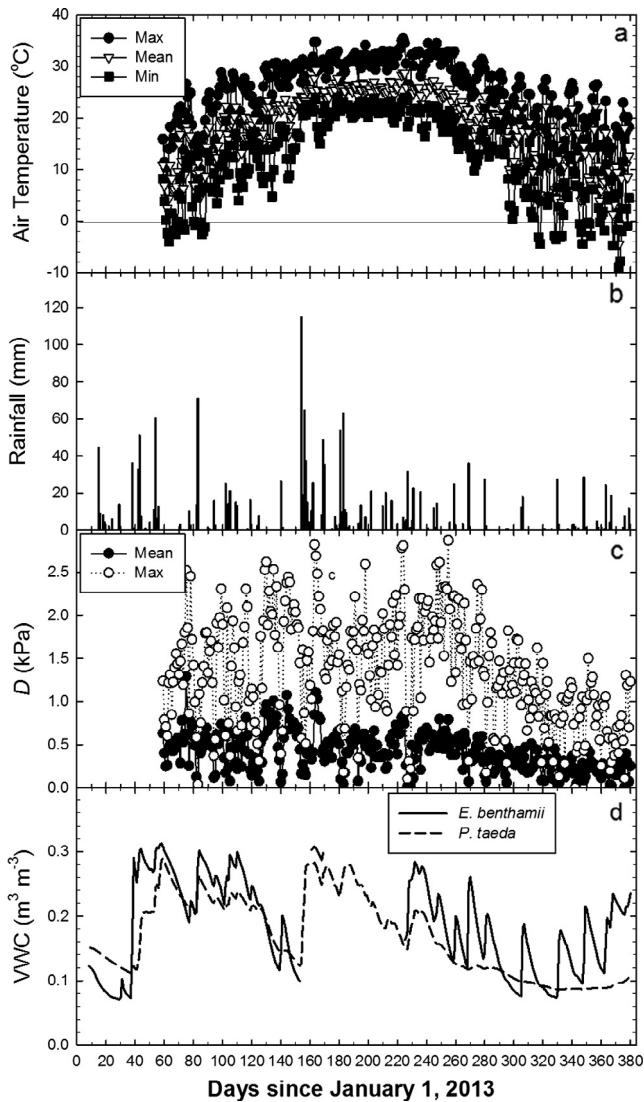
Fig. 4. (a) Daily minimum, mean, and maximum temperature, (b) daily precipitation, (c) mean and maximum air vapor pressure deficit (D), and (d) daily averaged volumetric water content at a 30 cm soil depth.

was 114 kg tree^{-1} compared to 44.7 kg tree^{-1} in pine ($P < 0.001$). There was no difference in annual diameter increment; however, there was a difference in the seasonal pattern of diameter growth. Pine completed 95% of annual diameter growth by early October (Fig. 5), whereas, in *Eucalyptus*, diameter growth was continuous throughout the year. Annual stem biomass increment was 22.9 kg tree^{-1} for *Eucalyptus* compared to 11.8 kg tree^{-1} for pine ($P = 0.013$). Sapwood area was similar between species, however, *Eucalyptus* trees had significantly lower leaf area than pine and thus a significantly higher A_s:A_l (Table 1). Pine exhibited a lower LAI$_p$ in February (2.03) and higher LAI$_p$ in September (3.71) than *Eucalyptus* (February: 2.40; September: 2.92).

3.3. Tree sap flux (F_d) and tree water use (E_t)

Eucalyptus had a higher daily F_d than pine (Fig. 6a). Mean daily F_d was 196.6 and 105.8 g cm^{-2} day^{-1} for *Eucalyptus* and pine, respectively (SE = 2.4, $P < 0.001$). The seasonal pattern of F_d differed with species. Both species reach a spring maximum around DOY 130–150 (May–June) when F_d occasionally exceeded 400 g cm^{-2} day^{-1} in *Eucalyptus* and 200 g cm^{-2} day^{-1} in pine. Afterward, F_d gradually
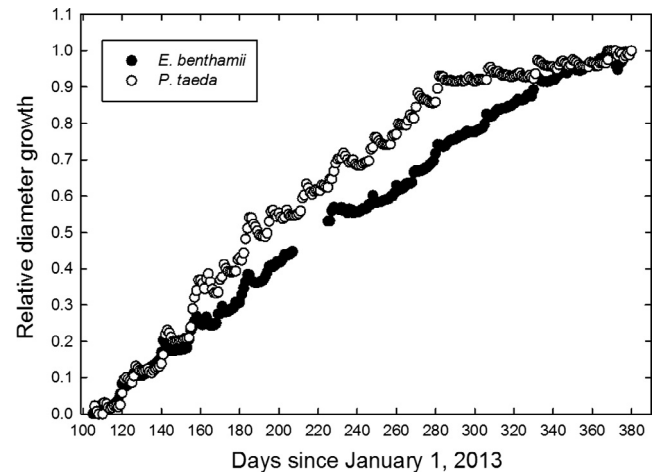

Fig. 5. Relative diameter growth of *Eucalyptus* and pine measured with automated dendrometer bands. Measurements began in mid-April. Each point represents the average of nine and six trees for *Eucalyptus* and pine, respectively.

declined in pine. In contrast, *Eucalyptus* exhibited a bimodal pattern where following the seasonal maximum, F_d declined during the summer, then increased again in late summer and fall. The largest species differences in F_d (40–60%) occurred during this period (DOY 240–260). High rates of F_d in both species were also measured between DOY 330–360. These days corresponded to large daily swings in temperature where nighttime freezing was followed by warm days. High F_d may indicate stomatal damage and loss of stomatal regulation. Two strong freeze events occurred in early January

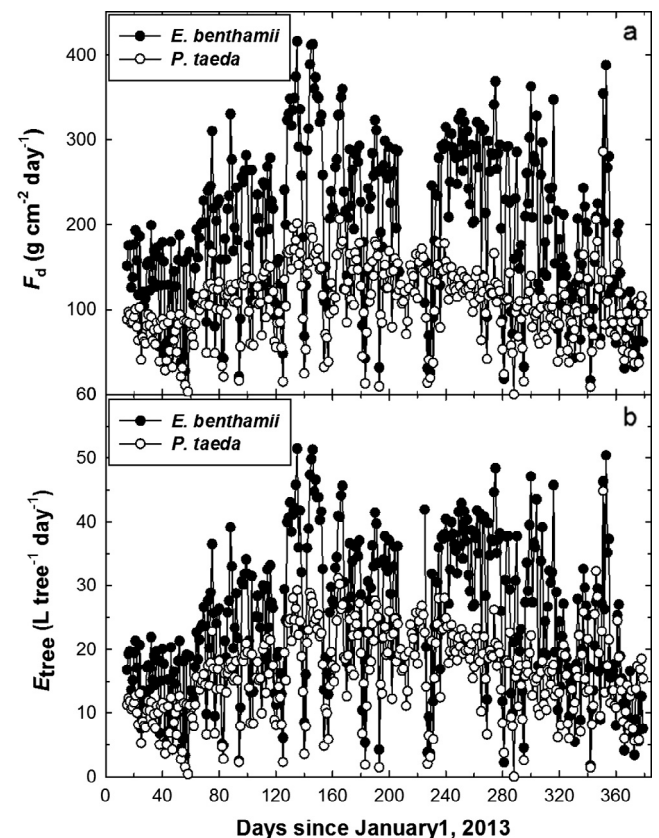**Fig. 6.** (a) Mean daily sap flux density (F_d, g m^{-2} day^{-1}) and (b) tree transpiration E_t (L tree^{-1} day^{-1}) in a 9-year-old *Eucalyptus* and loblolly pine trees. Each point is the mean of 12 (*Eucalyptus*) and 11 (pine) trees.

where minimum temperatures were $<-7\,°C$ (DOY 372–373) and caused crown damage in *Eucalyptus*. Following these events, F_d was lower in *Eucalyptus* than pine.

Total daily water use per tree or tree transpiration (E_t) was also greater in *Eucalyptus* (Fig. 6b). Mean daily E_t was 24.6 L day^{-1} compared to 15.2 L day^{-1} for pine (SE = 0.46, $P < 0.001$). Mean daily tree transpiration per unit ground area ($E_{t,g}$) was 3.11 and 2.17 mm day^{-1} for Eucalyptus and pine, respectively (SE = 0.04, $P < 0.001$). Although, *Eucalyptus* trees were larger, there was no species difference in A_s, thus greater tree water use in *Eucalyptus* was due to greater F_d. Nocturnal water use ($E_{t,night}$; PAR < 5 µmol m^{-2} s^{-1}) was slightly higher in *Eucalyptus* (0.45 L day^{-1}) than pine (0.33 L day^{-1}) (se = 0.04, $P = 0.030$), which corresponded to 2.34 and 2.97% of daily water use in *Eucalyptus* and pine, respectively. $E_{t,night}$ was linearly correlated with D over a range of 0.05–0.55 kPa (pine: $R^2 = 0.18$, $P < 0.001$; *Eucalyptus*: $R^2 = 0.29$, $P < 0.001$).

The contrasting seasonal patterns of F_d and E_t are better illustrated using monthly-accumulated E_t (m^3 H$_2$O month^{-1}) (Fig. 7). Monthly average E_t was 39% higher for *Eucalyptus* (0.76 m^3 H$_2$O month^{-1}) than pine (0.46 m^3 H$_2$O month^{-1}) (SE = 0.06, $P < 0.001$). There was a significant Species x Month interaction ($P < 0.001$) where the largest monthly difference between species occurred in May ($P < 0.001$), September ($P = 0.003$), and October ($P = 0.001$).

Annual E_t was 9.13 m^3 H$_2$O year^{-1} for *Eucalyptus* compared to 5.79 m^3 H$_2$O year^{-1} for pine (SE = 0.82, $P = 0.048$) and tree $E_{t,g}$ was 1077 and 733 mm year^{-1} (SE = 81, $P = 0.007$) for *Eucalyptus* and pine, respectively. Annual stem biomass increment and annual tree E_t increased linearly with initial stem mass measured at the beginning of the study (Fig. 8a and b). Interestingly, pine had greater E_t than *Eucalyptus* at similar stem biomass. Accounting for differences in stem mass, there was no significant difference in E_t (*Eucalyptus*: 7.3, pine: 7.6 m^3 H$_2$O year^{-1}; SE = 1.0, $P = 0.872$). Annual E_t was linearly related to stem mass growth in *Eucalyptus* and pine (Fig. 8c); although, there was no significant difference in the regression ($P > 0.05$). Tree water use efficiency (WUE, kg m^{-3} H$_2$O) was calculated as the quotient of annual stem growth (kg year^{-1}) and annual tree water use (m^{-3} H$_2$O year^{-1}). There was no significant relationship between WUE and tree size (data not shown); however, WUE was negatively correlated with tree height (Fig. 8d). Accounting for species differences in tree height, WUE was significantly greater in *Eucalyptus* (2.86 kg m^{-3} H$_2$0 year^{-1}) than in pine (1.72 kg m^{-3} H$_2$0 year^{-1}) (SE = 0.22; $P = 0.004$).

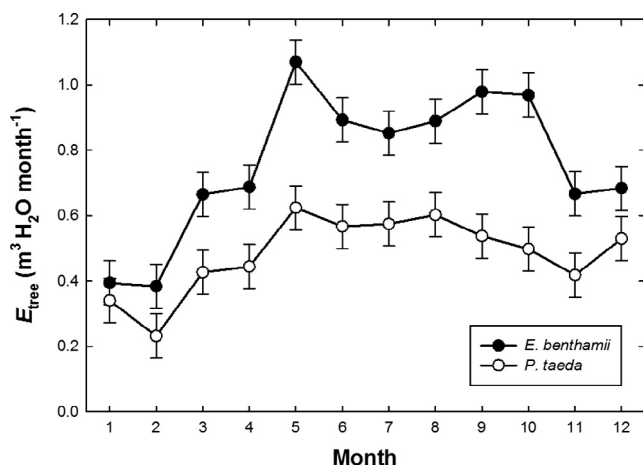**Fig. 7.** Monthly mean tree transpiration (E_t, m^3 tree^{-1} month^{-1}) in 9-year-old *Eucalyptus* and loblolly pine. Data are least square means and standard errors (*Eucalyptus*; $n = 12$; pine: $n = 11$).

3.4. Leaf transpiration (E_l), canopy stomatal conductance (G_s), and sensitivity to D

Despite large seasonal variation in VWC, there was no relationship between daily F_d and VWC in pine ($P > 0.05$). In *Eucalyptus*, daily F_d was negatively correlated with VWC ($P < 0.001$); however, the relationship was weak ($R^2 < 0.10$) (data not shown). This pattern was driven primarily by high daily F_d in late spring (DOY 140–160) when VWC was relatively low (Fig. 5).

Leaf transpiration and G_s, were estimated for early spring (April, DOY 91–120) and late summer (September, DOY 244–273) corresponding to periods of near minimum and maximum LAI$_p$ (Fig. 1). Mean mid-day (1000–1400 h) E_l and G_s were significantly greater in *Eucalyptus* than pine (Table 2); however, there was a Species x Season interaction (E_l: $P = 0.004$; G_s: $P = 0.007$). Species differences in E_l and G_s were non-significant in April while rates in *Eucalyptus* were much greater in September. The diurnal patterns of E_l and G_s differed between species and seasons. For example in April, both species had similar diurnal patterns of E_l and G_s, and maximum G_s occurred several hours before maximum E_l (Fig. 9c and e). In September, maximum daily E_l and G_s in pine occurred earlier in the day relative to D than in *Eucalyptus*, and G_s declined more rapidly in pine (Fig. 9d and f). The time lag between E_l and D created a hysteresis in the relationship where at similar D; E_l was greater in the morning than in the afternoon. (Fig. 9c and d inset). The magnitude of the hysteresis was a function of the time lag between maximum E_l and D. Average across all days, the time lag between maximum E_l and D was similar between species in April (*Eucalyptus*: 1.38, pine: 1.52 h; SE = 0.10, $P = 0.802$); however, the time lag increased in September for both species and was significantly greater in pine (*Eucalyptus*: 1.89, pine: 2.56 h; SE = 0.10, $P < 0.001$).

Canopy stomatal conductance decreased with D (Fig. 10a) and there was a significant Species x Season effect in the response to D ($G_{s,ref}$, $P = 0.004$; $-m$, $P = 0.011$) (Table 3). There was no difference between species in $G_{s,ref}$ or $-m$ in April, however *Eucalyptus* had significantly greater $G_{s,ref}$ in September. There was a significant linear relationship between $-m$ and $G_{s,ref}$ in both species ($P < 0.001$) (Fig. 10b) and pine had a higher ratio between $-m$ and $G_{s,ref}$ than *Eucalyptus* in April (pine: 0.845; *Eucalyptus*: 0.611; $P = 0.002$) and September (pine: 0.830; *Eucalyptus*: 0.675; $P = 0.003$). At similar $G_{s,ref}$, pine appeared to have greater sensitivity to D than *Eucalyptus*.

4. Discussion

4.1. TDP calibration

In pine, the standard Granier equation estimated cumulative water use within 13% of the observed measured with the potometer and the relationship between $F_{d,g}$ and $F_{d,p}$ was near unity. In contrast, the standard equation severely underestimated sap flow in *Eucalyptus*. A highly significant but nonlinear correlation between $F_{d,g}$ and $F_{d,p}$ enabled adjustment of $F_{d,g}$ to predict sap flow in *Eucalyptus* (Fig. 3b). The TDP probes appear to lose sensitivity when $F_{d,p}$ exceeded 250 g m^{-2} s^{-1}. These results suggest that for some species, potometers may generate high sap flow rates, perhaps because resistance at the soil-root interface to water uptake is not a factor (i.e. cut trees may have artificially high sap flow rates that do not occur in trees with intact roots). This same factor could also influence potometer based sap flow estimates in pine; however, alteration of the resistance at the soil-root interface did not appear to influence water uptake in pine in the same way it affected *Eucalyptus*. The extent to which the potometer-based calibration procedure affected results in our study is unknown;
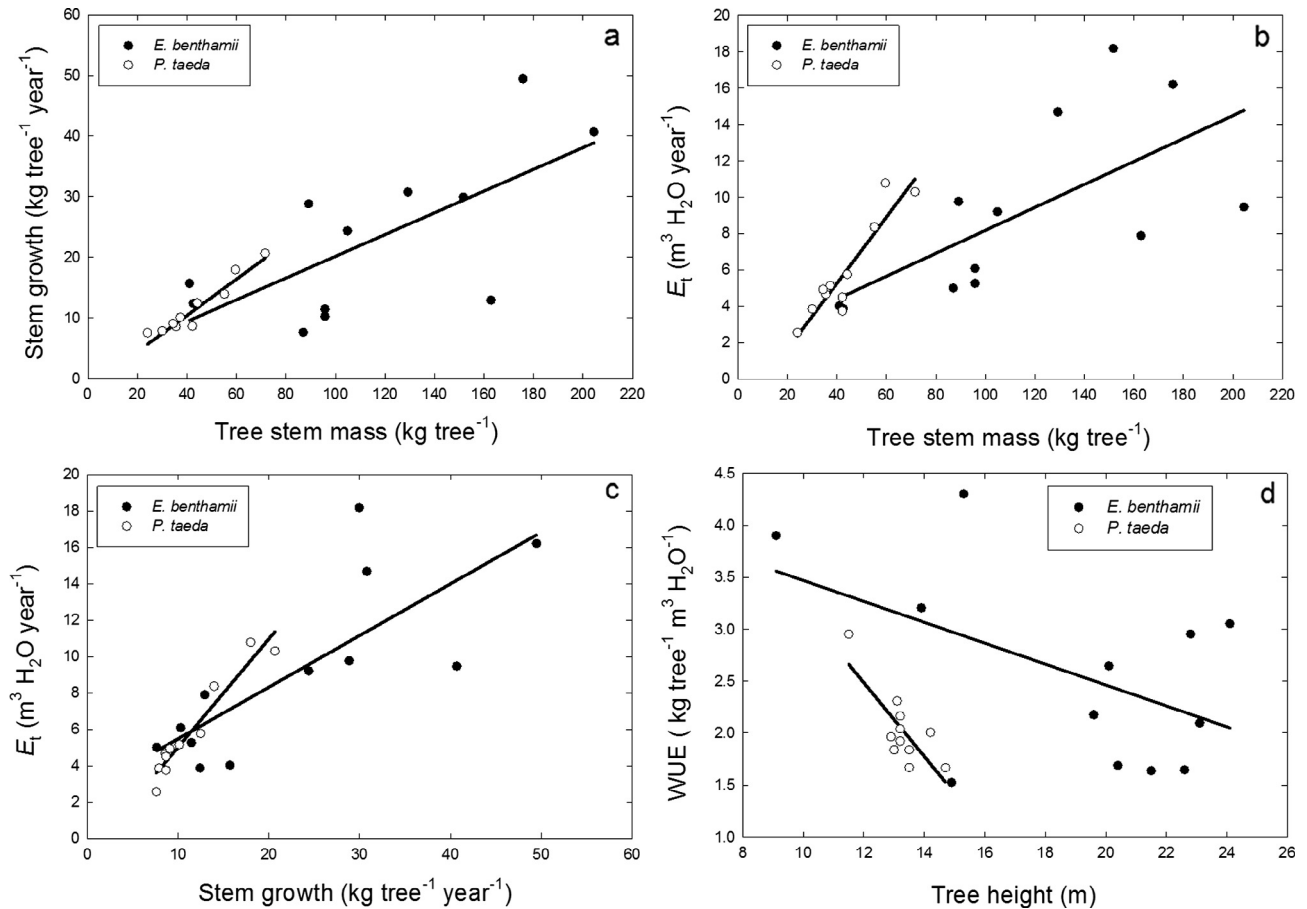
Fig. 8. Relationship between (a) stem biomass growth and initial stem biomass, (b) annual tree water use and initial stem biomass, (c) annual tree water use and stem biomass growth, and (d) tree water use efficiency (WUE) and tree height.

Table 2
Mean mid-day (1000–1400 h) leaf transpiration (E_l, mmol m^{-2} s^{-1}) and canopy stomatal conductance (G_s, mmol m^{-2} s^{-1}; PAR > 1200 μmol m^{-2} s^{-1}) measured in April (DOY 91–120) and September (DOY 244–273). Data are LSMEANs and standard error in parentheses.

Month	Species	E_l	G_s
April	E. benthamii	2.11 ab[1]	188.6 a
	P. taeda	1.84 b	165.7 a
September	E. benthamii	2.80 a	198.3 a
	P. taeda	1.29 c	84.4 b
		(0.26)	(20.7)

[1] Within column, means followed by different letters denote significant differences at α = 0.05.

however, $F_{d,g}$ above 120 g m^{-2} s^{-1} was rarely observed in intact *Eucalyptus* trees. Our results corroborate other studies that suggest the original Granier calibration underestimates sap flow in *Eucalyptus*. For example, a fivefold underestimate from the standard equation was observed in four year-old *E. grandis × urophylla* hybrids (Hubbard et al., 2010) and, similar to our study, a threefold underestimate was observed for three-year-old *E. globulus* and *E. nitens × globulus* hybrid trees (Rubilar et al., 2017).

4.2. F_d, E_t and WUE

Mean daily E_t and $E_{t,g}$ were significantly greater in *Eucalyptus* than pine. Although *Eucalyptus* trees were larger, there was no significant difference in A_s, therefore greater E_t in Eucalyptus was due greater F_d. Pine E_t and $E_{t,g}$ were similar to plantation grown trees in

other studies in the Southern US. For example, Samuelson and Stokes (2006) reported 1.5 mm day^{-1} for control plots and 2.4 mm day^{-1} for plots receiving weed control, irrigation, and fertilization. Gonzalez-Benecke and Martin, 2010) reported maximum E_t of 2.6 and 4.3 mm day^{-1} for non-irrigated and irrigated stands, respectively, although the trees were much larger than in our study. Higher rainfall (19% greater than average) could have driven higher E_t (Stape et al., 2004). We are aware of no sap flow estimates of E_t for *E. benthamii*; however, the values measured in this study are comparable with sap flow rates reported for other plantation grown *Eucalyptus* species (Whitehead and Beadle, 2004). Dye (2013) reported daily E_t for nine-year-old *E. grandis* that ranged between 2.0–7.5 mm day^{-1} and 30.9–64.3 L tree^{-1} and under high D could exceed 90 L tree^{-1}.

There was a Species x Month interaction where *Eucalyptus* exhibited a seasonally bimodal pattern in daily E_t that did not occur in pine. This seasonal pattern in E_t is likely related to differences in growth dynamics. For example, diameter growth in pine ceased by early fall (DOY 280), whereas, stem growth in *Eucalyptus* was continuous throughout the study (Fig. 5). Furthermore, we observed 20–60% greater net photosynthesis in *E. benthamii* compared to *P. taeda*, and *Eucalyptus* was able to maintain high photosynthetic rates even in winter (*K. Johnsen unpublished data*). *Eucalyptus* had significantly higher $E_{t,night}$; however, the proportion of total daily flow was low (<3.5%) in both species. Nocturnal transpiration was lower than reported for *E. grandis* (5%, Benyon, 1999) and *P. taeda* (11%, Oishi et al., 2008), although the trees were larger in these studies. Gonzalez-Benecke et al. (2011) found that E_{night} ranged from 6–8% of total daily water use in *P. elliottii* and *P. palustris*.
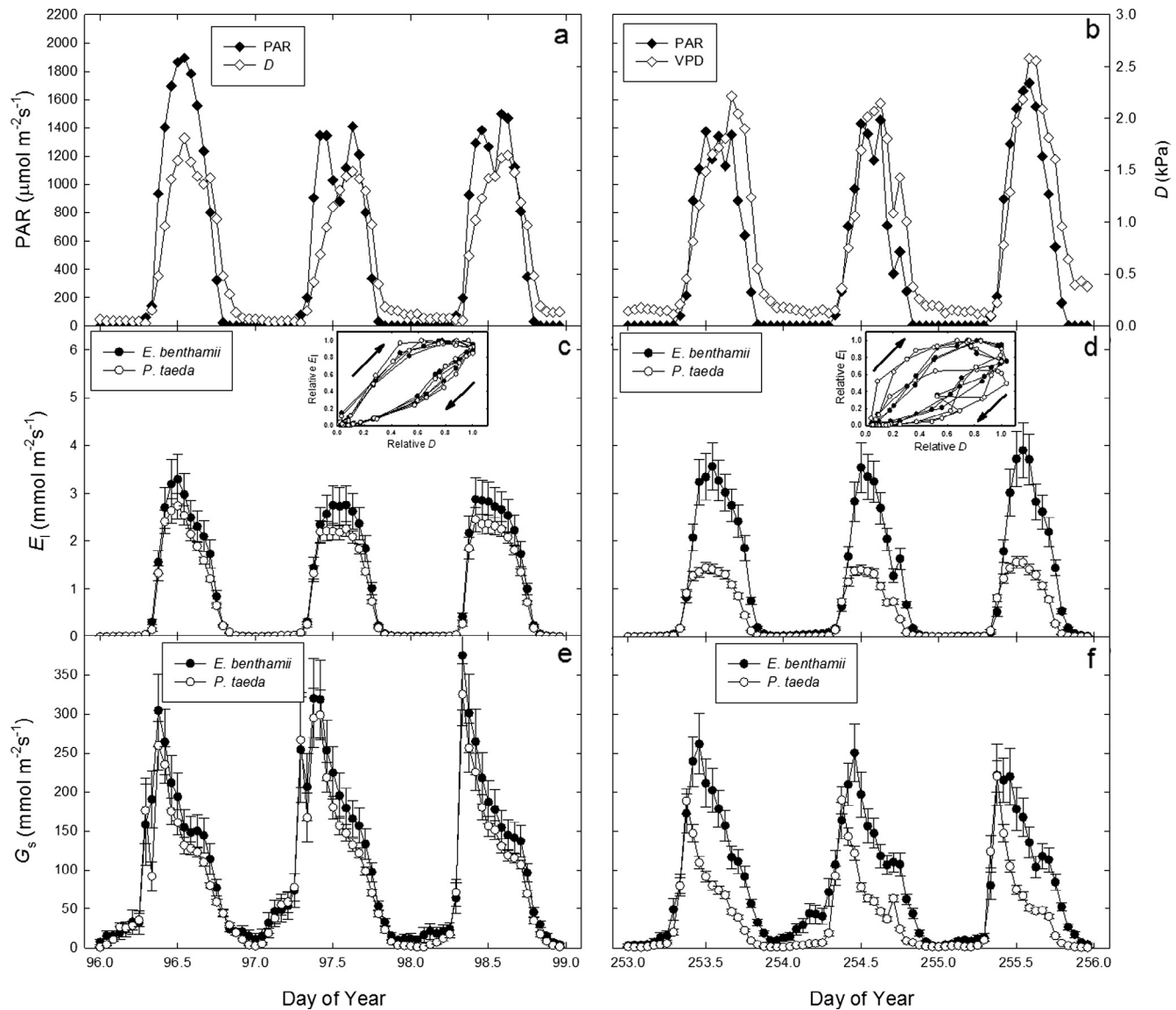
Fig. 9. Diurnal patterns of photosynthetically active radiation (PAR), vapor pressure deficit (D), transpiration per unit leaf area (E_l) and canopy stomatal conductance (G_s) for three consecutive days in April (panels a, c, and e) when LAI is near a seasonal minimum and in September (panels b, d, and f) when LAI is at a maximum. For E_l and G_s, each data point is the mean (±SE) of 12 (*Eucalyptus*) or 11 (pine) trees. Insets in panels c and d show the diurnal time course (arrows) in the relationship between E_l and D.

On an annual basis, *Eucalyptus* trees used 32% more water ($9.1 \text{ m}^3 \text{ H}_2\text{O year}^{-1}$, $1077 \text{ mm year}^{-1}$) than pine ($5.8 \text{ m}^3 \text{ H}_2\text{O year}^{-1}$, 733 mm year^{-1}). This corresponded to 66 and 45% of annual precipitation for *Eucalyptus* and pine, respectively. Gonzalez-Benecke and Martin (2010) measured annual E_t of 930 mm in irrigated loblolly pine which was 54% of total input (precipitation + irrigation). Hubbard et al. (2010) found that monthly E_t ranged from ≈ 150 mm to over 250 mm during the growing season in five-year-old *E. grandis × urophylla* plantations. In these same stands, annual E_t was 1394 and 1779 mm in rain-fed and irrigated stands, respectively. Dye et al. (2004) reported annual E_t ranging from 900 to 1400 mm in *E. grandis × camaldulensis*.

Pine had greater E_t at similar stem mass than *Eucalyptus* (Fig. 8b). Accounting for differences in tree size, there was no significant difference in annual water use (*Eucalyptus*: 7.3, pine: 7.6 $\text{m}^3 \text{ H}_2\text{O year}^{-1}$). Differences in stand development stage may explain this response. The *Eucalyptus* was at more advance stage of development, while the pine stand was at an age and stocking (BA = 22 $\text{m}^2 \text{ ha}^{-1}$) where foliage biomass production, leaf area, and total tree water use had just stabilized (Albaugh et al., 2004;

Martin and Jokela, 2004). As stem mass increases, water use per unit stem mass should decrease. We found no relationship between WUE and stem biomass as reported in other studies (Forrester et al., 2012; Otto et al., 2014); however, there was negative correlation with tree height, which is consistent with increased stem hydraulic resistance in taller trees (Hubbard et al., 1999). Correcting for height effects, *Eucalyptus* trees were 40% more water use efficient than pine (Eucalyptus: 2.9; pine: 1.7 kg m^{-3} $\text{H}_2\text{O tree}^{-1}$). *Eucalyptus* WUE in this study was within the range reported for *Eucalyptus sp* (Albaugh et al., 2013; Hubbard et al., 2010; Forrester et al., 2010; White et al., 2016). Samuelson and Stokes (2006) reported WUE ranged between 1.18–1.62 kg m^{-3} H_2O in five year-old irrigated and fertilized loblolly pine.

4.3. Leaf transpiration (E_l) and canopy stomatal conductance (G_s)

Eucalyptus had greater E_l and G_s than pine; though, there was a significant Species × Season interaction. Leaf transpiration, G_s and response to D were similar between species in the spring; however,
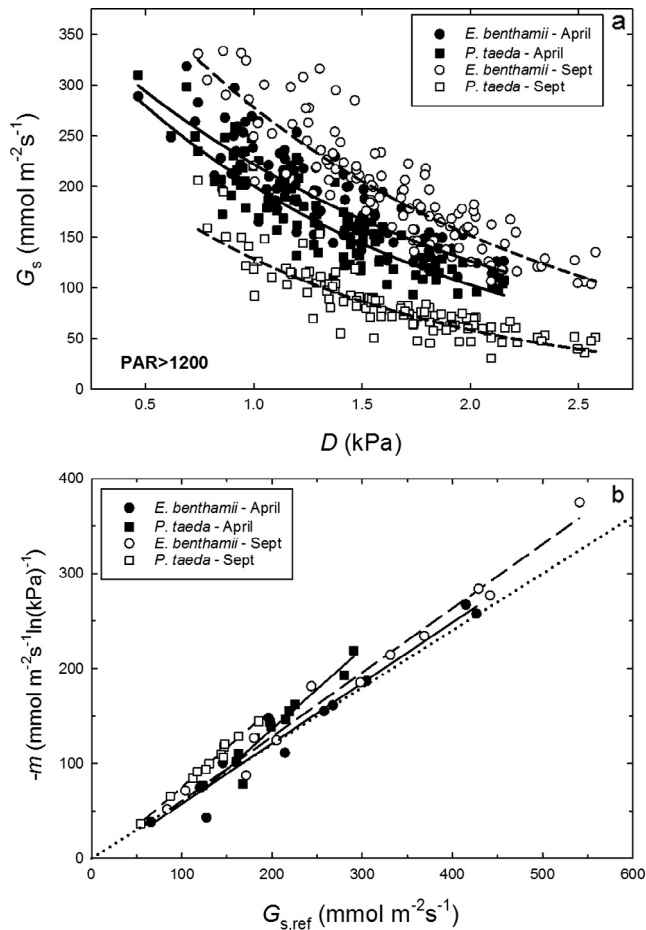
Fig. 10. Relationship between (a) canopy stomatal conductance (G_s) and air vapor pressure deficit (D) and (b) the sensitivity ($-m$) of canopy stomatal conductance to D and G_s at D at 1 kPa ($G_{s,ref}$) in nine-year-old *Eucalyptus* and pine. In panel a, data are at PAR > 1200 μmol m^{-2} s^{-1}. Each data point is the mean of 12 (*Eucalyptus*) or 11 (pine) trees. The dotted line is the theoretical 0.6 ratio between $-m$ and $G_{s,ref}$ (Oren et al., 1999).

Table 3
Parameter estimates for canopy stomatal conductance response to vapor pressure deficit (D) (Eq. (4)) when D > 0.75 kPa and PAR > 1200 μmol m^{-2} s^{-1}. G_{ref} is reference stomatal conductance and $-m$ is the rate of decrease in G_s per unit of D. Data are LSMEANS and standard error in parentheses.

Month	Species	G_{ref}	$-m$
April	*E. benthamii*	230.6 ab[1]	142.7 ab
	P. taeda	201.9 bc	137.7 ab
September	*E. benthamii*	283.1 a	184.4 a
	P. taeda	129.9 c	99.9 b
		(27.7)	(18.9)

[1] Within column, means followed by different letters denote significant differences at α = 0.05.

in September E_l and G_s increased in *Eucalyptus* while the opposite was observed in pine. As expected, there was a curvilinear relationship between G_s and D, and G_s sensitivity to D varied with species and time of year. Understanding species differences in G_s is critical as it controls E_l and is tightly linked to carbon assimilation (Franks and Farquhar, 1999). Oren et al. (1999) analyzed $G_{s,ref}$ and $-m$ across a range of species and found that $-m/G_{s,ref}$ = 0.6 and theorized that isohydric species maintain this ratio to regulate a minimum leaf water potential to prevent excessive E_l and xylem

cavitation. Averaged across season, $G_{s,ref}$ and $-m$ was greater in *Eucalyptus*; however, at similar $G_{s,ref}$, pine had greater sensitivity to D as indicated by the significantly greater $-m/G_{s,ref}$ in pine (0.84 vs 0.62 for pine and *Eucalyptus*, respectively). In pine, $-m/G_{s,ref}$ was significantly greater than the theoretical 0.6 which contrast with other studies for this species (Ewers et al., 2000; Samuelson et al., 2008; Gonzalez-Benecke et al., 2011). Values greater than the 0.6 proportionality may result from poor atmospheric coupling or high ratio between boundary layer and stomatal conductance (Oren et al., 1999).

The contrasting patterns between species in E_l, G_s, and response to D are likely due to species differential response to soil moisture and to different seasonal patterns of tree leaf area. We found little or no relationship between F_d and soil moisture probably because soil VWC rarely reach a limiting level. Reductions in canopy conductance in loblolly pine usually do not develop until plant available soil water falls below 30% (Gonzalez-Benecke and Martin, 2010). In our study, this threshold would be at 0.14 VWC, which did not occur for much of the growing season. However, this not to say the soil moisture had no effect on tree water use. Diurnal changes in E_l typically lag behind D creating a clockwise hysteresis pattern where at a similar D, E_l is greater in the morning than in the afternoon (Meinzer et al., 1997). The magnitude of the hysteresis is a function of lag time between E_l and D and has been attributed to low soil hydraulic conductivity and reduced stem capacitance (i.e. stored water) (O'Grady et al., 1999). Analysis of the lag times showed that pine had a significantly greater lag time compared to *Eucalyptus* in September, when VWC ranged from 0.14–0.19 than in April when VWC ranged from 0.22–0.24. These results suggest that lower VWC in September may have affected water uptake and lowered stem capacitance to a greater extent in pine than *Eucalyptus*.

Seasonal leaf area dynamics may have also influence species differences in E_l and G_s. *Eucalyptus* LAI$_T$ increased 22% from spring to fall compared to an 83% increase in pine. The large increase in LAI$_T$ likely reduced A_s:A_l. Water transport is dependent on A_s:A_l, plant hydraulic conductivity, and leaf water potential (Whitehead et al., 1984), and G_s is sensitive to reductions in stem and leaf hydraulic conductivity (Meinzer, 2002). In order to prevent low leaf water potential and leaf damage, increased leaf area must be accompanied by a proportional increase in A_s, or a reduction in whole-tree and leaf hydraulic conductance (Whitehead, 1998). For example, Samuleson et al. (2006) showed that fertilizing young loblolly pine plantations resulted in a large increase in leaf area and A_s:A_l, but had no effect on G_s, tree hydraulic conductance, or leaf water potential. On the other hand, Ewers et al. (2000) found that increased leaf area in fertilized loblolly pine was accompanied by reduced A_s:A_l, but the trees maintained leaf water potential, primarily through decreased G_s and tree hydraulic conductance. In the current study, reduced E_l and G_s and the more rapid diurnal decline in G_s in pine observed in September suggest a seasonal adjustment in tree or leaf hydraulic conductance. The mechanism for increased *Eucalyptus* E_l and G_s in the fall is unknown.

Water use in fast growing *Eucalyptus* and loblolly pine plantations is strongly correlated to leaf area (Whitehead and Beadle, 2004; Samuelson et al., 2008). Myers et al. (1996) reported 22% higher rates of evapotranspiration in three-year-old plantations of *E. grandis* than in *P. radiata*. Similarly, Moreaux et al. (2012) found 25% higher E_t in five-year-old *E. gunni x dalrympleana* plantations compared to native *P. pinaster*. Species differences in water use were attributed to differences in stand growth, stage of development, and leaf area. Our results contrast with these studies. Annual E_t was 25% higher in *Eucalyptus*, similar to the above studies; however, while pine exhibited a larger seasonal range in LAI, average (winter + summer) LAI was similar between species (*Eucalyptus*: 2.66; pine: 2.87). Thus, differences in water use were largely a function of species differences in E_l and G_s

4.4. Species differences in evapotranspiration

We did not measure water loss from canopy interception or soil evaporation; however, these components can account for up to 10–45% of stand evapotranspiration (ET = E_t + interception + soil evaporation) and must be considered when evaluating the stand water balance and effects on off-site water yield. Interception varies widely depending on canopy architecture, stand LAI, and rainfall intensity. These factors make it difficult to generalize; however, because of crown architecture, leaf shape and display, conifers typically have greater interception losses than hardwoods (Cannell, 1999). Using published estimates of interception loss for *Eucalyptus* (11%, Soares and Almeida, 2001) and loblolly pine (15%, Sun et al., 2010), interception losses would be 179 and 245 mm, respectively. Under these conditions, species differences in stand ET (1256 vs 997 mm for *Eucalyptus* and pine, respectively) would be lower relative to tree-level E_t. On the other hand, soil evaporation is probably higher in *Eucalyptus* potentially offsetting species differences in interception. Benyon and Doody (2015) compared interception and soil evaporation across 18 plantations of *E. globulus* and *P. radiata* and reported higher interception but lower soil evaporation losses for pine such that the relative contribution of interception and soil evaporation was similar between species, 46–48% of precipitation.

Estimated pine ET and the ratio ET/P (0.61) is within the range reported for loblolly pine plantations with similar stem density and leaf area as the stand in this study (Amatya et al., 2006; Sun et al., 2010; Domec et al., 2012). High ET/P has been reported for fast growing *Eucalyptus*. Almeida et al. (2007) estimated that ET of *E. grandis* in Brazil over a 6-year rotation used 95% of precipitation. Similarly, Cabral et al. (2010) reported that ET/P ranged from 0.82 to 0.96 in a young clonal *E. grandis x urophylla* plantation and Abichou et al. (2012) estimated ET/P of 0.81 for *E. amplifolia*. Under well-watered, closed canopy conditions, forest evapotranspiration can equal PET (Rutter, 1968). It was unlikely that these stands experienced drought as precipitation was well above average during the growing season. However, it is unknown how E_t and ET would differ under drought conditions. *Eucalyptus* spp. are typically deeper rooting than pine (Canadell et al., 1996) and can often rely on groundwater to drive E_t (Morris and Collopy, 1999) under dry conditions.

4.5. Implications

Our results suggest that young *Eucalyptus* plantations will have greater WUE than pine; however, because of greater growth potential, E_l, and G_s, total water use will be higher. Furthermore, *Eucalyptus* will likely be managed on shorter rotations (6–8 years) and will have greater cumulative water use over successive rotations compared to conventionally managed pine with longer rotations (15–25 years). Thus, species conversion from pine to *Eucalyptus* may adversely affect off-site water yield. The scale and location of plantation establishment will determine impacts on water yield at the catchment or landscape level. For example, Vose et al. (2015) evaluated stand- and regional-level implications of converting forest from pine to *Eucalyptus* on water yield across the southern United States (plant hardiness zones 8b and higher). Accounting for species differences in E_t (Penman-Monteith equation) and site variation in climate and hydrology, they concluded that converting pine to *Eucalyptus* could reduce stand-level water yield by up to 250 mm year^{-1} (48%) on some sites. Base on economic factors of *Eucalyptus* cultivation, Wear et al. (2015) concluded that less than 3% of the potential land base would be used for *Eucalyptus* production. At this scale, the likely impacts of *Eucalyptus* on regional water supplies would be small. Nevertheless, higher absolute water use by intensively managed *Eucalyptus* forests could have negative local-scale impacts on stream flow or ground water

reserves in water limited or ecologically sensitive areas (Albaugh et al., 2013; Vose et al., 2015).

5. Conclusions

We found that *Eucalyptus* trees had 94% greater stem growth, 32% greater tree water use (E_t), and 40% greater WUE than pine supporting part of our hypothesis. Species difference in WUE was likely a function of different carbon allocation strategies as *Eucalyptus* trees appeared to have poorer stomatal regulation of E_t. Differences in LAI were small, thus greater E_t in *Eucalyptus* was largely due to higher E_l and G_s. *Eucalyptus* and pine trees exhibited different stomatal behavior to D. While *Eucalyptus* had higher average $G_{s,ref}$, at a similar $G_{s,ref}$, pine had greater sensitivity to D probably due to seasonal changes in hydraulic architecture. These patterns were observed when precipitation was above normal with most of the excess rainfall occurring during the growing season. Consequently, low soil moisture and high D rarely occurred. Species-specific variance in E_t and the response of E_l and G_s to D may differ under water limited conditions. A better understanding of species differences in G_s and response to D and soil moisture is critical as it controls E_l and is tightly linked to carbon assimilation.

We only measured E_t, but the question of which species has greater impact on water resources must consider losses from canopy interception and soil evaporation. Potentially greater pine interception losses may minimize species differences in stand-level water use. A better understanding of E_t, interception, and evaporation within a stand developmental context is important for modeling water use and predicting species effects on stand water dynamics under short rotation culture.

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