Measured and predicted changes in water use of Eucalyptus nitens plantations following high-intensity thinning.

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Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation

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Summary We investigated changes in the pattern of water use of an 8-year-old *Eucalyptus nitens* (Deane and Maiden) Maiden plantation soon after thinning. Sap flow sensors using heat pulse technology were deployed across three stands thinned to a final density of 100, 250 or 600 trees ha^{-1} plus an unthinned control (1250 trees ha^{-1}). Changes in the relationship between tree size and daily water use were measured for 4 to 7 months after thinning. Thinning had no effect on sapwood water content. The increase in tree water use as a result of thinning was driven largely by significant changes in the radial pattern of sap velocity through the sapwood. The use of a canopy fraction factor in the Penman-Monteith equation to account for discontinuous canopies showed promise as a simple and effective method of scaling the model to predict transpiration from thinned plantations.

Keywords: heat pulse technique, Penman-Monteith equation, radial variation, sap flow, sapwood, transpiration.

Introduction

Water use by trees is driven by several environmental variables, including vapor pressure deficit (Oren et al. 1999), net radiation (Zotz et al. 1998), wind speed and temperature. Tree water use is also influenced by the availability of soil water within the rooting zone (Teskey and Sheriff 1996, David et al. 1997). The impact of these variables on the amount of water transpired depends on tree leaf area (Vertessy et al. 1995) and the stomatal behavior of the species (Hogg and Hurdle 1997, White et al. 1999*a*).

Thinning of *Eucalyptus nitens* (Deane and Maiden) Maiden plantations according to a commercial thinning regime (Forestry Tasmania 1999) converts the stands from closed to open canopies. Thus, after thinning, individual trees have greater access to site resources. In the absence of water stress, exposure of crowns to increased incident light should increase individual tree growth. However, the increase in growth rate of *Quercus petraea* (Matt.) Liebl. trees following thinning was attributed to an alleviation of tree water stress as a result of fewer trees extracting soil water (Bréda et al. 1995). Amounts of available water may be further enhanced after thinning by an increase in the amount of precipitation reaching the soil surface as throughfall (Aussenac and Granier 1988). Greater crown exposure leads to changes in vapor pressure deficit and boundary layer conductance. Vapor pressure deficit was shown to be the main environmental factor affecting transpiration of an isolated walnut tree (Green 1993). A greater boundary layer conductance per tree with an increase in tree spacing in *Picea sitchensis* (Bong.) Carr was caused by an increase in ventilation, i.e., wind speed (Teklehaimanot et al. 1991). The result is enhanced individual tree transpiration rates as found in *Chamaecyparis obtusa* Endl. after thinning (Morikawa et al. 1986). Conversely, reduced sap velocities in small trees within a stand can be attributed to limited light availability (Hunt and Beadle 1998). Because high-intensity thinning can alter a wide range of factors that influence growth, isolating the most important factor is difficult.

The heat pulse technique has been used to measure sap flow in a wide range of studies of the *Eucalyptus* genus (Dunn and Connor 1993, Hatton et al. 1998, Hunt and Beadle 1998, Benyon et al. 1999, O'Grady et al. 1999). The accuracy of the technique has been demonstrated by cut-tree experiments (Olbrich 1991, Vertessy et al. 1997). In addition, techniques for minimizing error in scaling point sap velocity measurements to whole-tree sap flow have been developed (Hatton et al. 1990, Zang et al. 1996). In the current study, we used the heat pulse technique to examine patterns of tree water use under ambient conditions in a recently thinned *E. nitens* plantation. Although water use of eucalypts is generally proportional to tree or crown size (Vertessy et al. 1995, Hunt and Beadle 1998, O'Grady et al. 1999), it has been suggested that this relationship may not apply in thinned stands where the trees are experiencing a rapid change in environment (Teskey and Sheriff 1996). We tested the hypothesis that, following thinning, water use by retained trees is greater than by similarly sized trees in an unthinned stand and therefore thinning does not cause a proportional reduction in plot transpiration.

Materials and methods

Trial site and experimental design

The thinning trial was established in an *E. nitens* plantation at Creekton in southeastern Tasmania (43°21′ S 146°54′ E). The plantation is at an altitude of 120 m. The ex-native forest site has red-brown gradational soils formed on Jurassic dolerite. The 1914 regrowth of *Eucalyptus obliqua* L'Herit was clear-felled before 1989. The trial site was burned, windrowed with a bulldozer and rip-mounded (Turnbull et al. 1992). Pre-planting herbicide (6 kg ha^{-1} a.i. atrazine and 2 kg ha^{-1} a.i. amitrole plus 2 kg ha^{-1} ammonium thiocyanate) was applied aerially 6 weeks before planting. Just before planting, triplesuperphosphate (120 kg ha^{-1} of elemental phosphorus) was applied. The site was planted in 1989 (unknown seedlot from the western distribution of *E. nitens* in Victoria) at 3.5 × 2.0 m spacing (1429 trees ha^{-1}). A meteorological station (1990–1998 inclusive) was located about 500 m from the trial site. Mean annual rainfall is 1175 mm. The mean weekly maximum temperature is 19.2 °C and the mean weekly minimum temperature is 3.6 °C.

Three thinning treatments were applied; retention of 100, 250 and 600 trees ha^{-1} and an unthinned control. At the time of thinning (age 8 years), the stand density was 1256 trees ha^{-1}. Three replicates of the treatments were assigned in a randomized block design to plots of 30 × 25 m (0.08 ha). The trial site was thinned as part of a commercial mechanized thinning operation during August 1997. For each thinning treatment (except the unthinned control) every third row was removed to allow machine access. The remaining rows in each plot were thinned from below to reduce the plot to its final stand density.

Sap flow nomenclature

The sap flow nomenclature system recommended by Edwards et al. (1996) was adopted for this study. Sap velocity was used to describe the speed of water movement through the tree and was calculated using the known volume fractions of wood and water in the sapwood, and corrected for wounding. Heat pulse velocity (v_h), heat pulse velocity corrected for wounding (v'_h), and sap velocity (v_s) were expressed in units of mm s^{-1}. Sap flow (Q) was used to describe the volume of water movement through the stem and was calculated as the product of sap velocity and sapwood area, and was expressed in units of m^3 day^{-1}.

Sap flow measurements

Sap flow was measured across all thinning treatments with eight sap flow sensors (Model SF-100, Greenspan Technology, Warwick, Queensland, Australia). Measurements commenced 4 months after thinning and were carried out over a 3-month period during the 1997–1998 growing season. The trees in each thinning treatment were grouped into four classes based on diameter at breast height (DBH). Two reference trees were used in combination with a set of roaming sensors, deployed across thinning treatments and size classes for periods ranging from 3 to 14 days. One reference tree was randomly selected from the highest frequency DBH class in an unthinned plot. The other reference tree was randomly selected from the highest frequency DBH class in a nearby 250 trees ha^{-1} thinned plot. The two reference trees were each measured continuously with two loggers and four probesets, one in each of the northern, southern, eastern and western axes. Measurements began on December 8, 1997 and finished on March 2, 1998. Probes were reinstalled in the reference trees after 28-day periods.

Roaming sensors (one logger, two probesets per tree) were used on 47 trees across all four thinning treatments. Probeset 1 was inserted in the northerly aspect of each tree with thermistor pairs placed at depths of 15 and 10 mm inside the cambium. Probeset 2 was inserted in the easterly aspect of the tree so that the thermistor pairs were placed at depths of 10 and 5 mm inside the cambium. The probesets were at 1.3 m tree height and positioned so that no branch or bark deformity occurred within 0.15 m above or below the point of insertion. The heat pulse units were wrapped in reflective aluminum foil to act as a solar radiation shield. Each measurement used a 1.6-s heat pulse at 15-min intervals. Values of v_h greater than 150 s were considered to represent zero sap flow. The stem diameter at 1.3 m and total height of each of the sample trees were measured on completion of the experiment. Values of v_h were corrected for wounding effects (v'_h) by assuming a wound diameter of 2.2 mm (Swanson and Whitfield 1981) and using the method of Barrett et al. (1995).

Sapwood area and volume fractions

Four wood samples (one from each of northern, eastern, southern and western aspects) were taken at the completion of sampling of each tree to estimate sapwood area at the height of sap flow measurement. A 5-mm increment corer was used to extract the samples. Sapwood width was estimated by holding the diameter cores over a light table so that the sapwood vessels involved in water transport could be clearly seen as points of light. Mean sapwood width was combined with bark width and diameter over bark measurements to estimate sapwood area by subtraction.

Two additional cores (one each from northern and eastern aspects) were taken for gravimetric determination of the volume fractions of wood and water in the sapwood of each tree.

Radial variation

Sap flow variation in the radial axis of the tree was accounted for by measuring a sap flow profile in each of the roaming sample trees at the completion of the measurement period (after Zang et al. 1996). On warm clear days, probesets were inserted in the southern and western aspects of the tree. Radial profiles were constructed for each of these two axes by moving the sensors in 5-mm increments 2 min before the heat pulse was fired (10-min interval between pulses). The southern probeset was pushed into the tree, whereas the western probeset was pulled out of the tree. These profiles were used with corresponding point measurements from the northern and eastern axes to determine a correction coefficient for the routine point measurements (a mean of point to moving ratios, weighted by sapwood depth). The correction coefficient for northern and eastern stationary sensors was applied to the northern and eastern v_s values made at 10 mm under the cambium.

Weather data

Measurements of air temperature (T), relative humidity (h), vapor pressure deficit (D), wind speed (u) and rainfall (r) were made at a weather station established 500 m from the experimental site. A screened and ventilated Vaisala probe (Vaisala Oyj, Helsinki, Finland) measured T, h and D. Wind speed (u) was measured with a cup anemometer at a height of 6 m. Rainfall (r) was measured by a tipping-bucket rain gauge with a 0.2-mm bucket. A 21X data logger (Campbell Scientific, Logan, UT) was programmed to sense T, h, D, u and r every 5 min. Mean hourly T, h, and D and hourly totals of u and r were recorded. Technical problems were encountered at the weather station with the measurements of total solar radiation (I) and net radiation (R_n) during the sap flow measurement period. Consequently, I and R_n data from a weather station located at Lewisham (72 km from the experimental site) were used. At Lewisham, I and R_n were measured with an LI-200s pyranometer (Li-Cor, Lincoln, NE) and a Fritschen-type net radiometer (Model 3032, Qualimetrics, Sacramento, CA), respectively. A 21X data logger was programmed to sense I and R_n every 5 min. Hourly totals were recorded. A regression between R_n values from Lewisham and Creekton was statistically significant ($r^2 = 0.62$, $P < 0.0001$).

Plot transpiration

Tree sap flow measurements were integrated upward for daily stand-level transpiration (E_m):

$$E_m = L_j \left(\frac{\sum_{i=1}^{n} \frac{Q_{ij}}{A_{ij}}}{n} \right), \quad (1)$$

where L_j is leaf area index of the jth thinning treatment, Q_{ij} is daily sap flow of the ith tree in the jth thinning treatment and A_{ij} is leaf area of the ith tree in the jth thinning treatment. Values of A_{ij} were estimated from an allometric relationship between stem sapwood area at breast height and leaf area for *E. nitens* that was independent of thinning treatment (Medhurst et al. 1999). Values of L_j were obtained from LAI-2000 Plant Canopy Analyzer (Li-Cor) measurements during March 1998 (calibrated for *E. nitens* after Cherry et al. 1998).

Predicted daily transpiration rates (E_p) were calculated with the Penman-Monteith equation (Monteith 1965) as a submodel of PROMOD (Battaglia and Sands 1997), a process-based productivity model. Aerodynamic conductance, g_a, was estimated from the maximum boundary layer conductance observed in an irrigated *Eucalyptus globulus* Labill. and *E. nitens* plantation (White et al. 1999*a*). Estimates of canopy conductance, g_c, were made using a phenomenological model developed for *E. globulus* and *E. nitens* to consider the effect of D, T, I and water stress on maximum stomatal conductance (White et al. 1999*a*). Canopy transpiration was calculated from g_c by using a dimensionless coupling coefficient (Ω) (Jarvis and McNaughton 1986, White et al. 1999*b*):

$$\Omega = \frac{\beta + 1}{\beta + 1 + g_a / g_c}, \quad (2)$$

where:

$$\beta = \frac{\Delta\lambda}{c_p P}, \quad (3)$$

where Δ is rate of change of saturated water vapor pressure with temperature, λ is latent heat of vaporization, c_p is the specific heat of air and P is atmospheric pressure.

An imposed rate of transpiration (E_{imp}), assuming that air vapor pressure deficit (D) was imposed at the canopy surface ($\Omega = 0$), was calculated as:

$$E_{imp} = \frac{(c_p / \gamma) g_c D}{\lambda}, \quad (4)$$

where γ is the psychrometric constant.

An equilibrium transpiration rate (E_{eq}, $\Omega = 1$) was calculated as:

$$E_{eq} = \frac{\beta R_n}{(\beta + 1)\lambda}. \quad (5)$$

Parameters E_{imp} and E_{eq} were used to calculate E_p:

$$E_p = \Omega E_{eq} + (1 - \Omega) E_{imp}. \quad (6)$$

Daily measurements of maximum and minimum T, I and r were combined with L to run PROMOD. The effect of thinning was incorporated into the model by a simple canopy fraction factor (C_f). The C_f value was an estimate of the projected canopy area as a fraction of ground area based on a mean crown radius value of 2.0 m (J.L. Medhurst, unpublished data). In the model, C_f was used to scale up L of the thinned stand to that of a closed canopy (L_c):

$$L_c = \frac{L}{C_f}. \quad (7)$$

Parameter L_c was used in the model to make closed canopy predictions of daily transpiration (E_p'). Vales of E_p' were scaled back to E_p for each thinned stand based on C_f:

$$E_p = E_p' C_f. \quad (8)$$

Data analysis

Mean daily sap velocity was calculated across a 24-h period.

Sap flow was calculated as sap velocity multiplied by sapwood area. Mean daily sap velocity and sap flow for the roaming sample trees were regressed against values from the reference trees to estimate water use of sample trees for the entire measurement period. The reference tree that produced the stronger relationship was used. Although seasonal fluctuations in leaf area index of eucalypt species occur (Pook 1984), we assumed that leaf area remained constant during the experiment. The leaf area of each tree was used to estimate mean sap flow per unit leaf area (Q_l) across the 84-day measurement period.

Analysis of variance was used to assess the effect of thinning on volume fractions of wood (V_w) and water (V_h), mean daily sap velocity, sap velocity correction coefficients, and sap flow per unit leaf area. The GLM module in SAS (SAS Institute 1990, Cary, NC) was used for the analysis. The least squares method was used to determine means and standard errors. Post-hoc comparisons were carried out by Fisher's least significant difference test.

The effect of thinning treatment on the relationship between stem basal area and mean daily sap flow was investigated by regression analysis. A two-sided natural logarithmic transformation was carried out to ensure homoscedasticity of variance. A group regression procedure was used to test whether the deviance of the model was significantly increased by generalizing the slope and intercept across thinning treatments (McPherson 1990). Measured and predicted daily plot transpiration values for each thinning treatment were compared by paired *t*-tests.

Results

Tree characteristics

A similar range of tree sizes was sampled in each of the thinning treatments (Table 1). Tree leaf area (one-sided or projected) ranged from 10.0 to 99.6 m^2 for trees in the unthinned treatment and from 11.7 to 115.2 m^2 for trees in the thinned treatments. Sapwood area at breast height ranged from 4.9 to 21.0×10^3 mm^2 in trees from the unthinned treatment and from 4.5 to 23.3×10^3 mm^2 in trees from the thinned treatments (Table 2). Sapwood area was strongly related to stem cross-sectional basal area ($y = 0.23x^{0.87}$, $r^2 = 0.93$). This relationship was unaffected by thinning ($P > 0.05$). Values of V_w and V_h in the sapwood of trees in the unthinned treatment ranged from 0.24 to 0.31 and from 0.57 to 0.69, respectively. Values of V_w and V_h in the sapwood of trees in the thinned treatments ranged from 0.24 to 0.31 and from 0.60 to 0.69, respectively (Table 2). No significant difference in V_w or V_h was found with thinning treatment ($P > 0.05$).

Table 1. Summary statistics of diameter at breast height (DBH) for sampled trees in each thinning treatment.

Thinning treatment (trees ha^{-1})	n	Mean DBH (mm)	SE	Min. DBH (mm)	Max. DBH (mm)
100	11	212	12.8	133	271
250	13	197	14.0	127	279
600	11	190	12.4	131	255
Unthinned	12	187	13.9	118	283

Table 2. Summary statistics of tree size and sapwood parameters for the 47 sample trees at Creekton. Values in parentheses are standard errors. Abbreviations: V_h = volume fraction of water; V_w = volume fraction of wood.

Thinning treatment (trees ha^{-1})	Mean sapwood		Mean V_h	Mean V_w
	Area ($mm^2 \times 10^3$)	Width (mm)		
100	13.9 (1.5)	25 (2)	0.63 (0.01)	0.28 (0.01)
250	11.7 (1.4)	23 (1)	0.64 (0.01)	0.29 (0.01)
600	10.4 (1.2)	21 (1)	0.65 (0.01)	0.28 (0.01)
Unthinned	10.5 (1.4)	21 (1)	0.63 (0.01)	0.29 (0.01)

Radial variation in sap velocity

Maximum v_s with depth usually occurred between 10 and 20 mm (e.g., Figure 1). A comparison of northern and eastern values generally showed higher v_s at the northern aspect. Radial variation in v_s for similarly sized trees differed among thinning treatments (Figure 1). The correction coefficients calculated for the northern aspect at a depth of 10 mm ranged from 0.20 to 2.26 for trees in the thinned treatments and from 0.52 to 1.79 for trees in the unthinned treatment. There was no significant difference between the correction coefficients calculated for the northern and eastern aspects ($P > 0.05$, paired *t*-test). Mean correction coefficient values increased with increasing thinning intensity (Table 3). The northern and eastern correction coefficients were significantly higher for trees in the 100 and 250 trees ha^{-1} treatments than for trees in the unthinned treatment ($P < 0.05$).

Reference tree water use

Mean daily sap flow (Q) of the reference tree in the unthinned treatment (stem diameter of 168 mm at start of measurement) was 3.3×10^{-2} m^3 day^{-1} (range from 0.9×10^{-2} to 5.2×10^{-2} m^3 day^{-1}). Mean daily Q of the reference tree in the 250 trees ha^{-1} treatment (stem diameter of 201 mm at start of measurement) was 6.0×10^{-2} m^3 day^{-1} (range from 1.3×10^{-2} to 9.5×10^{-2} m^3 day^{-1}). Both followed a similar pattern of transpiration across the 84-day measurement period (linear regression $r^2 = 0.60$; Figure 2a). The difference in Q between the two trees was reduced on completely overcast days (e.g., Days 4, 51 and 59). Daily Q_l was higher for the reference tree in the 250 trees ha^{-1} treatment than for the reference tree in the unthinned treatment throughout most of the measurement period. However, this difference was greater during periods of low rainfall (e.g., Days 25–50 when total rainfall = 10 mm) (Figure 2b). Mean daily Q_l for the unthinned treatment reference tree was 1.0×10^{-3} m^3 m^2 day^{-1} (range from 0.3×10^{-3} to 1.6×10^{-3} m^3 m^2 day^{-1}). Mean daily Q_l for the reference tree in the 250 trees ha^{-1} treatment was 1.2×10^{-3} m^3 m^2 day^{-1} (range from 0.3×10^{-3} to 1.9×10^{-3} m^3 m^2 day^{-1}). The reference trees

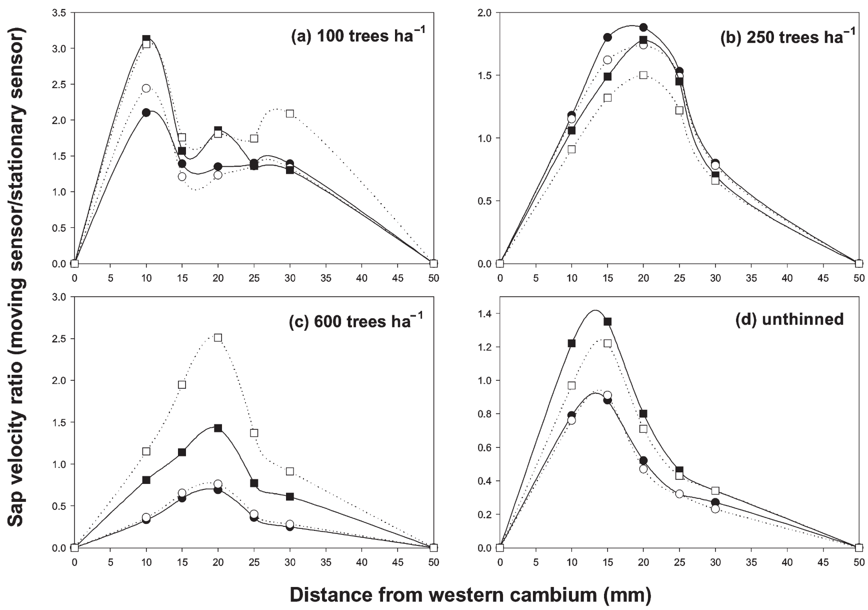

Figure 1. Examples of sap velocity ratio profiles for trees from the second DBH class in the (a) 100 trees ha^{-1}, (b) 250 trees ha^{-1}, (c) 600 trees ha^{-1} and (d) unthinned treatments at Creekton. The moving sensor was located in the western axis. The ratios for the northern and eastern stationary sensors are shown. Symbols show 15 mm under northern cambium (●); 10 mm under northern cambium (○); 10 mm under eastern cambium (■); and 5 mm under eastern cambium (□).

showed differences in diurnal variation of Q_l during warm and sunny days (Figure 3a), whereas no differences were observed on cool and overcast days (Figure 3b).

Regressions of the daily sap velocity of sample trees against that of the reference trees were strong. The coefficients of determination (r^2) ranged from 0.47 to 0.99 but were generally high (> 0.80 for 34 of the 43 trees).

Sap velocity

A sample tree in the unthinned treatment that produced very high sap velocity values was considered an outlier and was omitted from further analysis. The tree was unrepresentative of the treatment, because it was located in a natural drainage line at the base of a slope. Within each treatment, mean sap velocity across the measurement period was independent of tree cross-sectional area ($P > 0.05$). The mean sap velocities of trees in the 100 and 250 trees ha^{-1} treatments (0.042 and 0.041 mm s^{-1}, respectively) were significantly higher than that of trees in the unthinned treatment (0.019 mm s^{-1}) ($P < 0.05$). The mean sap velocity of trees in the 600 trees ha^{-1} treatment (0.030 mm s^{-1}) was not significantly different from that of trees in the unthinned treatment.

Whole-tree water use

Mean daily sap flow was correlated with stem basal area at breast height (Figure 4, $P < 0.01$). The effect of thinning treatment was significant for the slope of the log–log relationship ($P < 0.05$).

Daily sap flows per unit leaf area (Q_l) from each treatment were compared. Trees in the 100 and 250 trees ha^{-1} treatments had a significantly greater Q_l than trees in the unthinned treat-

Table 3. Mean and standard error (SE) of sap velocity correction coefficients by thinning treatment at Creekton.

Thinning treatment (trees ha^{-1})	Northern aspect		Eastern aspect	
	Mean	SE	Mean	SE
100	1.25	0.12	1.10	0.09
250	1.16	0.13	1.00	0.08
600	0.83	0.10	0.89	0.07
Unthinned	0.77	0.12	0.71	0.06

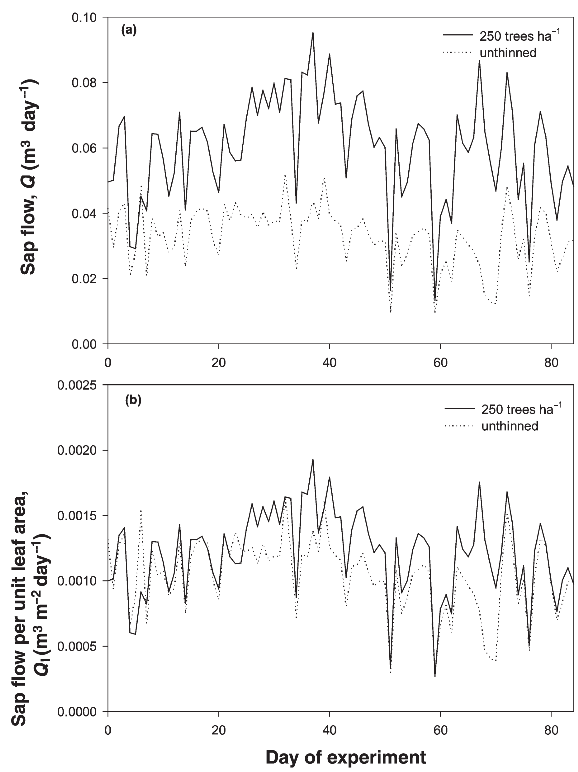

Figure 2. Daily (a) sap flow (m^3 day^{-1}) and (b) sap flow per unit leaf area (m^3 m^{-2} day^{-1}) for the reference trees at Creekton. Measurement commenced on December 8, 1997 and finished on March 2, 1998.

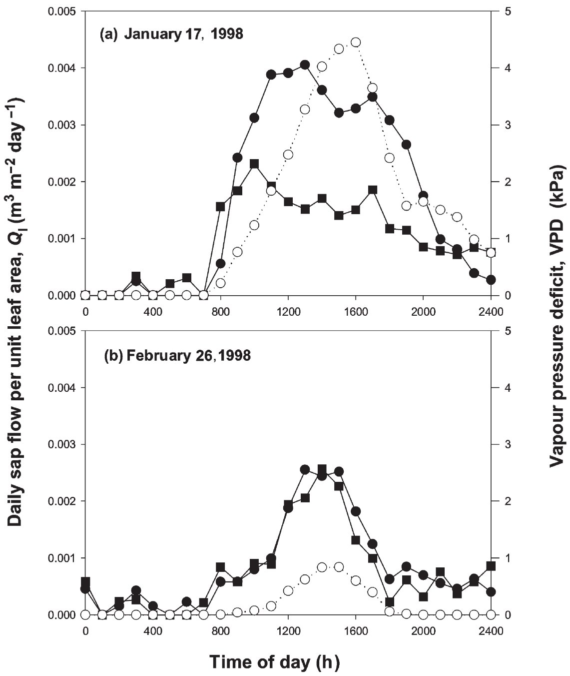

Figure 3. Diurnal variation in Q_l for the reference trees in the 250 trees ha^{-1} treatment (●) and the unthinned treatment (■) for (a) January 17, 1998 and (b) February 26, 1998. Variation in VPD is also shown (○).

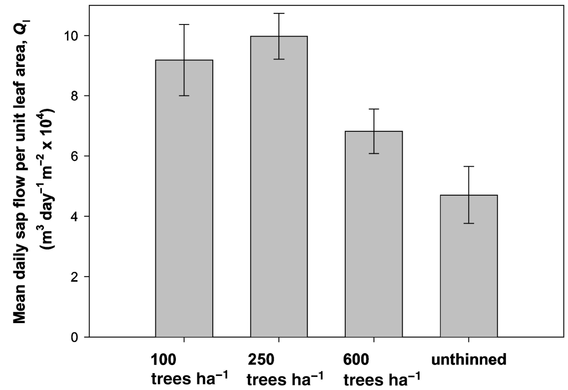

Figure 5. Mean daily tree sap flow per unit leaf area by thinning treatment at Creekton. Error bars show means ± standard errors.

ment ($P < 0.05$). Trees in the 600 trees ha^{-1} treatment had similar Q_l to trees in the unthinned treatment (Figure 5).

Plot transpiration

Mean daily plot transpiration (E_m) of the unthinned stand at Creekton was 2.6 mm day^{-1}. Maximum and minimum measured rates were 4.0 and 0.6 mm day^{-1}, respectively. Mean E_m of the 100, 250 and 600 trees ha^{-1} thinning treatments were 0.6, 1.0 and 1.4 mm day^{-1}, respectively. This represented 23, 36 and 55%, respectively, of the mean transpiration rate of the unthinned stand. The change in daily stand transpiration with mean daily VPD was minimal beyond VPD values of about 0.3 kPa (Figure 6).

Predicted daily plot transpiration (E_p) was considerably higher than measured values (E_m) on days of high maximum temperature and high mean VPD (Figure 7); e.g., during Days 37, 45 and 56, which were characterized by a mean daily temperature of 31.9, 28.8 and 32.3 °C, respectively, and a mean daily VPD of 0.75, 0.67 and 1.10 kPa, respectively. Daily E_p was 0.8, 1.3, 2.1 and 2.8 mm for the 100, 250, 600 trees ha^{-1} and unthinned treatments, respectively.

Total rainfall during the 84-day measurement period was 230 mm. Total E_m (218 mm) and E_p (235 mm) for the unthinned stand during this period were similar to total rainfall. Total E_m for the 100, 250 and 600 trees ha^{-1} treatments during this period were 50, 84 and 118 mm, respectively. Total E_p for the 100, 250 and 600 trees ha^{-1} treatments during this period were 67, 109 and 177 mm, respectively.

Discussion

Changes in the relationship between tree size and daily water use were found 4 months after thinning. These changes were

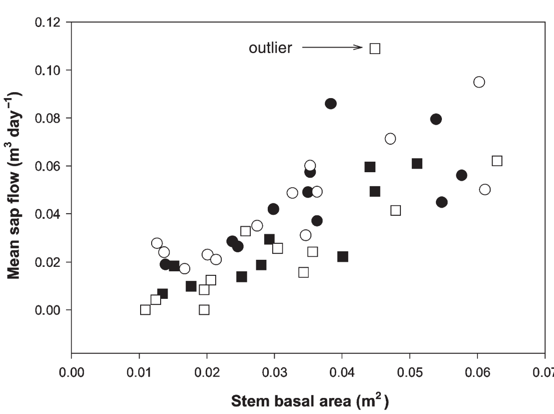

Figure 4. Relationship between mean daily sap flow and stem basal area (over bark) by thinning treatment (● = 100 trees ha^{-1}, ○ = 250 trees ha^{-1}, ■ = 600 trees ha^{-1} and □ = unthinned). The outlier was not used in the regression analysis.

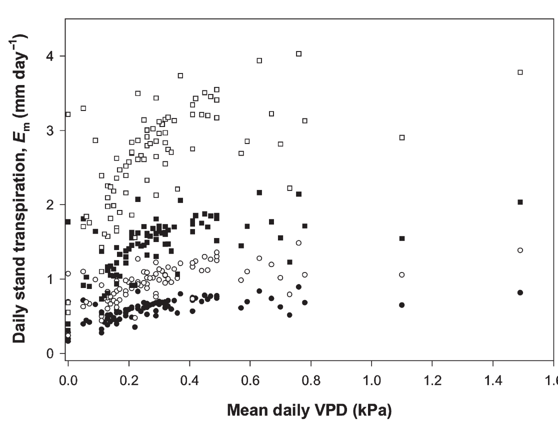

Figure 6. Measured daily stand transpiration as a function of mean daily vapor pressure deficit (● = 100 trees ha^{-1}, ○ = 250 trees ha^{-1}, ■ = 600 trees ha^{-1} and □ = unthinned).

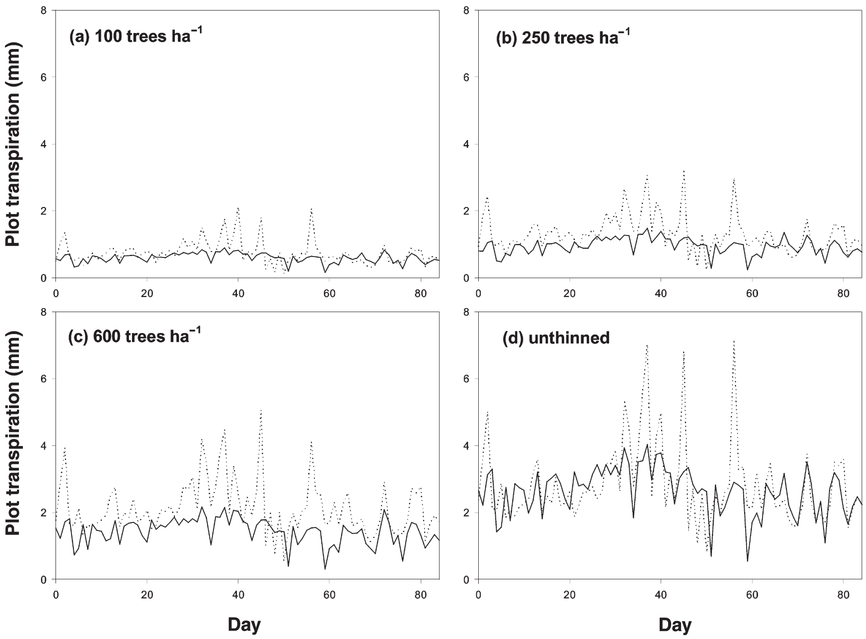

Figure 7. Measured (solid line) and predicted (dotted line) daily plot transpiration for the (a) 100 trees ha^{-1}, (b) 250 trees ha^{-1}, (c) 600 trees ha^{-1}, and (d) unthinned treatments at Creekton from December 8, 1997 to March 2, 1998. Measured transpiration rates are from sap flow sensors. Predicted transpiration rates are from Equations 2 to 8.

driven largely by differences in the radial variation of sap velocity with thinning treatment. For *Eucalyptus* stands not undergoing rapid change in leaf area index, strong and consistent relationships between tree size and water use have been reported (Calder et al. 1992, Hatton et al. 1995, Vertessy et al. 1997, Hunt and Beadle 1998, O'Grady et al. 1999). The suggestion of Teskey and Sheriff (1996)—that proportional water use by large and small trees, in terms of leaf area, may not apply in recently thinned stands—was supported by our findings. A major alteration in crown structure or root patterns and volume between the thinning operation and the measurement period is unlikely, because of the initially slow growth response to thinning (Medhurst et al. 2001). This suggests that the changes in transpiration after thinning were determined primarily by changes in climatic demand (Green 1993) or by physiological responses to an increase in soil water availability, or both (Calder 1992).

We found large radial variation in sap velocity. Radial variation in sap velocity has been found previously in *E. nitens* (Hunt and Beadle 1998) and in other *Eucalyptus* species (e.g., Dunn and Connor 1993, Hatton et al. 1995, Zang et al. 1996). Failing to account for this variability could lead to large errors in estimates of tree and stand water use (Wullschleger and King 2000). Integrating point measurements of v_s to Q for each tree was a major source of potential error in our study. Based on the correction coefficient method of Zang et al. (1996), the maximum mean potential error in Q of individual trees with stratified sampling was 29% (Table 3). This was in close agreement with the value of 25% found by Hatton et al. (1995) for an *E. populnea* Muell. woodland. It is worth noting that the mean correction coefficient of the unthinned stand in our study (0.77) was almost identical to that measured by Zang et al. (1996) in an *E. globulus* plantation (0.78).

Although between-tree variation was large, sampling intensity and stratification was sufficient to show that thinning a closed-canopy stand altered radial profiles of sap velocity. Without considering radial variation in sap velocity, the sap flow of trees after thinning was underestimated, whereas the sap flow of trees in unthinned stands was overestimated. A more complete understanding of the change in radial variation is required before heat pulse technology can be used to compare tree water use under different management strategies. The technique of weighting heat pulse velocity measurements by the area of sapwood sampled (e.g., Hatton et al. 1990) may not be suitable in studies where different management scenarios are being compared.

The causes of radial variation in v_s are not well understood (Wullschleger and King 2000), although several hypotheses have been proposed. Studies have shown a decrease in sapwood water content with depth, but this alone does not account for the change in v_s with depth (Phillips et al. 1996, Wullschleger and King 2000). Dye et al. (1991) suggested that the inner sapwood is the primary conduit for water supply to the older, lower branches of a tree. They postulated that increased shading or branch death means that the sap velocity of the inner sapwood declines because of lower transpirational demand. A high correction coefficient value using the method of Zang et al. (1996) implies that a high proportion of sapwood area is contributing to water transport. We found that mean correction coefficient values increased with increasing thinning intensity for the first 8 months after applying the treatment. The improvement in light conditions after thinning results in increases in photosynthetic activity of the lower section of the crown (Wang et al. 1995, Peterson et al. 1997), which is likely to increase transpirational demand from this section of the crown. If the inner sapwood is the primary conduit for supplying water to the lower section of the crown, the increase in correction coefficients with thinning lends support to the theory of Dye et al. (1991).

Axial variation in sap velocity was negligible in our study.

Differences in sap velocity by aspect have generally been observed in trees with asymmetrical crowns (Vertessy et al. 1997, Hunt and Beadle 1998). As this study was carried out in a recently thinned plantation, it would be reasonable to expect symmetrical crowns across all thinning treatments. However, in the longer term, asymmetrical crowns can develop after thinning (Medhurst and Beadle 2001) and differences in sap velocity with respect to aspect may develop.

In the short term, thinning did not alter sapwood characteristics. The volumetric fractions of water and wood in the sapwood of the sampled trees were similar across thinning treatments. These fractions have also been shown to be constant with age in *E. regnans* (Dunn and Connor 1993). Higher correction coefficients with thinning may be indirect evidence of an increase in the hydraulic conductivity of sapwood (k) soon after thinning. Despite increases in soil water potential and transpiration from tree crowns soon after thinning, studies have shown that leaf water potential has remained generally unaffected (Cregg et al. 1990, Ginn et al. 1991). For this to occur, k must be increased by thinning (Jarvis 1976, Whitehead et al. 1984). An increase in k with soil water availability was inferred from long-term studies in *E. nitens* (White et al. 1998), and higher radial variation in sap flow in *E. nitens* was found in trees subjected to strong interspecific competition (Hunt and Beadle 1998). A decline in k with distance from the cambium was found for two *Populus* species; however, axial direction affected k, with the side of the trees receiving greater sunlight having significantly greater k (Edwards and Booker 1984). Shelburne and Hedden (1996) found radial variation in k for *Pinus taeda* L. that could not be explained by anatomical differences in tracheids. They attributed the greater proportion of viable sapwood in trees with reduced competition to the ability to obtain sufficient amounts of nutrients and water to maintain an effective sapwood area. In addition, the ability of trees to reverse xylem embolisms, and thus restore k, has been shown (Hacke and Sauter 1996, Borghetti et al. 1998). We observed changes in the radial variation of v_s, and hence permeability of the sapwood, soon after thinning. Such a change may be a feedback mechanism to avoid development of deleterious leaf water potentials after thinning (Jarvis 1976).

Differences in the daily sap flow per unit leaf area (Q_l) of the reference trees in the 250 trees ha^{-1} and unthinned treatments were greatest on days of high sap flow. These days were characterized by high VPD. Technical difficulties associated with solar radiation measurements at the Creekton site meant that the relationship between transpiration and solar radiation could not be investigated. However, transpiration rates of thinned and unthinned stands are closely related to both solar irradiance and VPD (Morikawa et al. 1986). Increases in Q_l in response to thinning are likely to be caused, in part, by an increase in the amount of intercepted radiation and changes in conductance on a tree-basis. A linear increase in tree boundary layer conductance with increasing tree spacing was found in *P. sitchensis* (Teklehaimanot et al. 1991). In addition, there is an improvement in soil water availability per tree as a result of thinning (Bréda et al. 1995). Although we did not measure soil water, it is notable that the thinning-induced increases in Q_l were greatest during periods of low rainfall.

The value of E_p for the unthinned stand was in close agreement with E_m, except for days of high maximum temperature and VPD. The reason for lower than expected values of E_m across all thinning treatments on these days is unknown. Although within the range of transpiration rates for *Eucalyptus* stands (Vertessy et al. 1995), mean E_m of our unthinned stands was lower than some reported rates of mean transpiration in *E. nitens* plantations (Honeysett et al. 1992), but similar to the rates reported for *E. nitens* by Hunt and Beadle (1998). The tendency for the model to slightly over-predict transpiration rates may have been caused by the use of solar radiation data that were not collected at the Creekton site. We used a mean crown radius value, but more direct measurements of tree domain have shown promise as a scalar of sap flow measurements to stand-level water use (Hatton et al. 1995). Therefore it is likely that a direct measure of canopy projection area in each thinning treatment would have improved the accuracy of E_p in our study. Despite the data limitations of our study, the canopy fraction factor in the Penman-Monteith model showed promise as a simple and effective method for scaling the model to predict transpiration from thinned stands.

We conclude that k of *E. nitens* may rapidly adjust in response to changes in growing conditions. Greater water conduction through the inner sapwood after thinning treatment provides evidence of changes in transpiration patterns within the crown. Hence, knowledge of changes in crown structure, particularly the rate of leaf area recovery after thinning, is important for longer-term prediction of stand water use. The enhanced rates of water use in retained trees following thinning would be expected to decline to the rates in trees in an unthinned stand over time as the stand approaches or regains full canopy closure. Teskey and Sheriff (1996) found that water use was proportional to leaf area 5 years after thinning in a *Pinus radiata* D. Don plantation. The rate of return to a common tree size–water use relationship across the range of thinning treatments at Creekton is likely to depend on the rate of canopy closure.

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