Differences in water use between mature and post-fire regrowth stands of subalpine *Eucalyptus delegatensis* R. Baker

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ABSTRACT

We estimated plot level water use from sap flux measurements over a 9-month period, in post-fire regrowth and mature plots of *Eucalyptus delegatensis* R. Baker (Alpine ash) in high elevation catchments near Falls Creek, Victoria, Australia, seven years after a major stand-replacing bushfire. Water use was more than double (460 ± 100 mm year^{-1} more) in regrowth as compared to mature plots, whereas sap flux was similar between age classes. This difference in water use reflected 72% greater sapwood area index and 35% greater leaf area index in regrowth than in mature plots. A small part of the difference in water use can be attributed to nocturnal transpiration, which was greater in regrowth than in mature plots ($10.3 \pm 0.8\%$ vs $7.3 \pm 0.8\%$ of diel totals). As evaporative demand was 41% greater in mature than in regrowth plots, these data suggest mean transpiration rate and stomatal conductance per unit leaf area were approximately 1.6 and 2.3 times greater, respectively, in the regrowth. However, mid-day leaf water potential and photosynthetic capacity were similar in both age classes. Evaporative demand was the primary environmental driver of water use in all cases, whereas soil moisture was not a strong driver of either water use or canopy conductance (estimated as sap flux/evaporative demand). Together, our results suggest (a) stand water use rapidly recovers after fire in these high elevation forests and quickly surpasses rates in mature stands, confirming projections by Kuczera (1987) for lower-elevation Mountain Ash (*E. regnans*) forests and highlighting the potential impact of tree water use on water yield in the first decade of forest regeneration after fires, and (b) stomatal conductance and sapwood area/leaf area ratio are both less in tall, older Alpine ash trees, whereas leaf water status and photosynthetic capacity appear to be sustained – consistent with predictions from optimisation theory but not Pipe-Model Theory.

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1. Introduction

Water use by forest vegetation often declines with age (e.g., Vertessy et al., 2001; Delzon and Loustau, 2005; Ryan et al., 2006). The reasons differ among sites and species, and may involve reductions in stomatal conductance or leaf area index (Ryan et al., 2006). A consequence of the age-related decline in water use is that, following major disturbance such as a stand-replacing fire, the new, rapidly growing young trees may use more water than the older trees that they have replaced (Langford, 1976; Kuczera, 1987; Cornish, 1993; Hornbeck et al., 1993). This has potentially serious implications in regions that depend on runoff from forested catchments for urban or agricultural water supply.

Forested catchments in the mountains of southeastern Australia supply water to millions of people in the region and to an agricultural industry that is vital to the region's economy. These forests are subject to periodic stand-replacing fires, notably in 1939 and more recently in 2003 and 2006. Previous studies estimated the impact of such fires on catchment water balance using runoff data from high-rainfall (1700–1800 mm year^{-1}) and moderate-elevation ($\sim$900 m) sites 50 km east of Melbourne, dominated by mountain ash (*Eucalyptus regnans* F. Muell). Langford (1976) reported a decline in streamflow from catchments in this area after the 1939 fires, beginning 3–5 years after the fires. Kuczera (1987) later analysed 41 years of post-fire runoff data for these catchments, and fitted those data with an empirical model (the "Kuczera curve") that predicted a rapid but saturating decline in yield – reaching 50 and 100% of maximum yield reductions at an average of 7.6 and 33 years after the fires, respectively. Long-term yield reductions (after 15 years) in these mountain ash forests were shown to result from reduced stand sapwood area and to a lesser extent from reduced leaf area, by measurements of sap flow

and stand characteristics by Dunn and Connor (1993) and Vertessy et al. (1995; 1997; 2001). Other eucalypt forests have shown varying trends, however. For example, yield reductions were found 2–3 years after logging in old-growth eucalypt forests of central New South Wales (Cornish, 1993), whereas Cornish and Vertessy (2001) reported an initial increase in water yield after logging in mixed eucalypt forested catchments near Sydney, and a clear reduction in yield only after 12 years. A paired catchment study in mixed eucalypt forest also found an initial increase in yield followed by a clear reduction after 4 years for patch-cut sites, but an initial yield increase with no subsequent reduction in thinned sites (Lane and Mackay, 2001).

It is clear that the dynamics and extent of changes in water yield from eucalypt forests after disturbance vary widely. Although differences in transpiration of regrowing trees probably contribute to this variation, the role of tree water use in the early phase of post-fire regeneration remains poorly understood, because few studies have directly measured tree water use in the first decade after fires. Most direct measurements have been carried out for fairly short periods and/or in older stands (Dunn and Connor, 1993; Vertessy et al., 1995, 1997; Roberts et al., 2001; Vertessy et al., 2001; Eichelmann et al., 2005). Moreover, little is known about the response of stand water use to fire in *Eucalyptus delegatensis* R. Baker (Alpine Ash) – a higher elevation species that dominates a large part of the Victorian Alps, which supply most of the region's agricultural water – and a recent modeling study of water yields from catchments including *E. delegatensis* highlighted the need for better information about stand water use in the early post-fire years (Lane et al., 2010). *E. delegatensis* is also of particular interest because it is one of a minority of tree species (McDowell et al., 2002; Mokany et al., 2003; Macfarlane et al., 2004) that apparently contradict the "pipe model theory" of Shinozaki (1964a,b), which predicts tall trees produce more sapwood area per unit leaf area in order to counteract the burdens of height growth on water transport. Measurements of the structural, physiological and environmental controls on water use in relation to stand age in Alpine Ash may inform ongoing debate about the physiological ecology of transpiration in tall trees (Ryan and Yoder, 1997; Koch et al., 2004; Ryan et al., 2006).

The objective of this study was to measure plot water use in subalpine (∼1300 m) stands of Alpine Ash that germinated after the 2003 fires, and to compare these results with data from adjacent mature stands that survived the fires. We measured sap flux with the heat ratio method (Burgess et al., 2001) in relation to environmental variables in 11 mature trees of AA (71 years old and 40–50 m tall) and 10 young trees (7 years old and 4–6 m tall) growing in monospecific stands in the Alpine National Park near Falls Creek, Victoria, Australia, and analysed results for 213 days from December 2009 to August 2010 (late spring to late winter), during which data were continuously available for all trees. To inform future attempts to predict effects of fire on stand water on a process basis, we also measured physiological variables (stomatal conductance, photosynthetic capacity and leaf water potential).

2. Materials and methods

2.1. Study sites

Our study sites are located near the town of Falls Creek (36° 51′ S, 147° 16′ E) in the Victorian Alps of Australia, approximately 230 km NE of Melbourne. The sites are in mountainous terrain in the upper Kiewa Valley, roughly 5 km N/NW of Falls Creek. The mature sites (M1 and M2) are stands that germinated following a major stand replacement fire in 1939. M1 is on a shallow, slightly

south-facing slope (i.e., facing away from the sun), and M2 is on a steeper, north-facing toe slope. Neither site has significant understory. The regrowth sites (R1 and R2) are in pure stands of alpine ash that germinated following major fires in December 2003. Plot size varied according to stem density and to our need to sample the range of stem diameters found in each stand. We thus used 50 × 50 m (2500 m²) plots in the mature stands and 10 × 10 m (100 m²) plots in regrowth stands. The fires that killed the previous mature trees at R1 and R2 were slowed and reduced in intensity at a track that formed a fire break between those sites and M1 and M2. R1 and R2 were located adjacent to M1 and M2, respectively, for logistical purposes, but they have different slopes and aspects than the mature sites. R1 is on a moderate east-facing slope and R2 is on a steeper north-facing slope. During a pilot study in 2006–2008, R1 and R2 comprised roughly equal populations of *E. delegatensis* and *Daviesia mimosoides*, but by the time of this study, *E. delegatensis* dominated and *Daviesia* represented a negligible portion of total leaf area. A third pair of sites, M3 and R3 (mature and regrowth, respectively), located between M1/R1 and M2/R2 on the same track, were chosen for measurements of crown water potential to permit crown access with a boom lift. Descriptive data for these sites are given in Table 1.

2.2. Atmospheric and soil measurements

Air temperature, relative humidity and soil relative water content were measured within each site using sensors supplied by ICT International (Armidale, NSW, Australia). Relative water content was measured using standing wave soil moisture sensors (MP406, ICT Int'l) installed at 20 and 50 cm depths at one location near the center of each plot. Temperature/relative humidity sensors (HT1, ICT Int'l) were placed in radiation shields 1 m above the ground. Air water vapour saturation deficit (evaporative demand) was calculated from air temperature and relative humidity. Onset of darkness (for estimation of nocturnal transpiration fraction; see below) was identified from photosynthetically active radiation, which was measured using a HOBO weather station (Onset Corp, Pocasset, MA, USA) at Howman's Gap, approximately 600 m from M1 and R1 and 1400 m from M2 and R2, at similar altitude.

2.3. Sap flux

We used the heat-ratio method (HRM), as developed and presented theoretically by Burgess et al. (2001) and validated by Bleby et al. (2004). For this study, we inserted one probe set at breast height (1.30 m) under the bark of each sample tree. To minimise bias due to azimuthal variation, probes were installed at the same azimuth in all trees. We characterised azimuthal variation by installing an additional five probe sets at 60° azimuth steps in one tree at each of the mature sites (M1 and M2), and accounted for this variation in our estimates of confidence intervals for plot-level sap flow. (We did not gauge azimuthal variation in trees at the regrowth sites because of the likelihood of bias arising from disproportionate anatomical damage if we were to install numerous probes in these small-diameter stems). Each probe set consisted of three probes, 0.13 cm in diameter and 3.5 cm in length, spaced 0.5 cm apart axially in the bole. A drill guide (ICT Int'l) was used to minimise errors in spacing and probe alignment. The centre probe contained a heater wire, and the upper and lower probes contained two thermocouples each, located 1.25 and 2.75 cm from the probe hub, which was situated at the outside of the stem after removing a small area of bark. In each tree, the thermocouple pair at 1.25 cm depth comprised the "outer sensor," and that at 2.75 cm depth comprised the "inner sensor." Heat pulses (40 or 50 J) were triggered by a 16-bit microprocessor unit

Table 1
Descriptive data for the sites used in this study. Environmental data are means for 02 Dec 2009–01 June 2010 (minus a gap from 21 Jan to 22 Feb 2010), the period used for analysis of environmental controls on sap flux. DBH, diameter at breast height (1.30 m); VPD, air vapour pressure deficit; RWC, relative water content.

Site name	Mature		Regrowth	
	M1	M2	R1	R2
Elevation/m	1300	1280	1290	1260
Slope/%	5–10	10–25	30–47	35
Aspect/°	196	0	0	35
Approx. mean height/m	40	45	5	5
Range of diameter at breast height/cm	29.1–82.5	25.2–86.0	1.8–11.0	1.5–10.8
Mid 50% of diameter at breast height/cm	42.2–57.1	41.8–56.5	4.2–8.3	4.3–7.5
Air temperature/°C	12.1	11.7	8.6	11.2
Relative humidity/%	9.7	9.3	9.1	10.6
Evaporative demand/kPa	0.44	0.45	0.27	0.36
Soil relative water content (20 cm)/%	22.3	24	29.2	21.3
Soil relative water content (50 cm)/%	21.0	21.2	27.5	35.8

attached to the tree adjacent to the probes, approximately 10 cm to the side of the probe insertion point, and temperature ratios were recorded 80 s after each pulse. Measurements were recorded every 30 min. The probe interfaces were connected to ICT SmartLogger dataloggers, powered by one or two 12-volt truck batteries that were continuously recharged by solar panels.

Raw heat pulse velocities were calculated using values of thermal diffusivity ($k = 2.18$–2.32×10^{-3} cm^2 s^{-1}) measured in one tree core at each of the four sites, and corrected for wounding using a homogeneous third-order polynomial (Burgess et al., 2001), assuming a wound diameter of 1.8 mm. The flux of xylem water through sapwood (this is "sap velocity on a total sapwood area basis" in the terminology of Edwards et al., 1997) was calculated by multiplying corrected heat pulse velocities by the bulk density and heat capacity of fresh wood, and dividing by the bulk density and heat capacity of sap (water) (Marshall, 1958; Burgess et al., 2001; Buckley et al., 2011). Fresh wood density and heat capacity were measured on cores from one tree at each site; the resulting conversion factors ranged from 0.701 to 0.759 (dimensionless) for mature trees, and from 0.742 to 0.816 for regrowth trees.

We could not fell trees or cut through stems to ensure zero-flow for probe calibration in mature trees because our sites are located within a national park. Instead, we estimated baselines *in situ* by analysing periods in which relative humidity remained above 99.5% for at least 24 h. The mean heat pulse velocity during the final 25% of the longest such period available for each sensor was taken as the baseline for that sensor. This assumes that refilling of depleted bole water stores is complete within 18 h – an assumption strongly supported by the time-course of sap flux on nights with low evaporative demand, as described previously (see Buckley et al., 2011). For consistency, we applied this same zeroing method to regrowth stands as well.

Single-point data gaps were filled by linear interpolation between the adjacent points; larger gaps were not filled. For sap flux data, high frequency noise was reduced by local weighted linear least squares smoothing (loess) with a 5-point window and a tri-cube weight function.

Additional details concerning the analysis of sap flux (partitioning sapwood area into inner and outer bands, separating transpiration from refilling of bole water stores, scaling sap flux measurements to the plot level, and generating 95% confidence intervals for scaled estimates of plot water use) are provided in Appendix A.

2.4. Sapwood area and leaf area

Sapwood area was estimated from two cores taken from each sample tree, and partitioned into "outer" and "inner" bands by

defining the boundary between these bands as the midpoint between outer and inner sensors (2.0 cm sapwood depth). Leaf area was estimated from point measurements made in each plot with hemispherical photography, following the method of Macfarlane et al. (2007). Within each stand, images were taken using a Nikon Coolpix 5700 digital camera located at 1.3 m height. Images were processed with the WINPHOT image processing tool (ter Steege, 1996). LAI was averaged for 10–11 images in each plot.

2.5. Physiological measurements

In November 2006 and January, February and November 2007, we measured aspects of leaf physiology in mature crowns and at two heights in regrowth crowns ("upper", within 50 cm of the crown top; and "lower", between 1.5 and 2 m below the crown top). These measurements include stomatal conductance (which was measured at two times of day: morning [8–11 am] and afternoon [1–3 pm], with a porometer [Decagon SC-1, Decagon, Pullman, WA, USA]), and photosynthetic capacity (carboxylation capacity, V_{m25}, and maximum potential electron transport rate, J_{m25}, both measured with an infrared gas analyser [Li-Cor 6400, Li-Cor, Lincoln, NE, USA]). Mature crowns were accessed by a tree climber who excised branches with a pole saw. Measurements were completed within 15 min of excision, and showed no consistent trends during that time (not shown). Conductance was measured for three leaves, chosen haphazardly. In regrowth plots, all three leaves were from different individuals, but for mature plots, the difficulty of crown access made this impossible, so all three leaves were from the same individual in each case. Photosynthetic capacity was measured for one leaf from one individual in each plot. Additional details for measurement of photosynthetic capacity are given in Appendix B.

In December 2009 and February and May 2010, we measured leaf water potential on three leaves of each of three individual trees, at predawn (5–6 am) and mid-day (12-1 pm) with a Scholander-type pressure chamber (PMS model 1000, PMS Instrument Co, Corvallis, OR, USA) at sites M3 and R3. Leaves were excised with clean razor blades and sealed in the pressure chamber for measurement within 20 s of excision.

2.6. Statistical analysis

We assessed differences in the measurements described above among age classes, months in the study and time of day where applicable, by analysis of variance and regression analysis. Further details are provided in Appendix C.

3. Results

3.1. Sap flux

We collected sap flux and environmental data for 534 days between March 2009 and November 2010. Because periods of available data differed among sites and sensors, statistical comparisons of sites using all available data may be biased. Comparative analyses therefore focused on 213 days (03 Dec 09–13 Aug 10, excluding a gap from 21 Jan 10 to 22 Feb 10) during which data were available for all sap flux sensors simultaneously. Analyses of environmental data and their effect on sap flux focused on 148 days (03 Dec 09–01 Jun 10, excluding the gap from 21 Jan 10 to 22 Feb 10), because data were unavailable for several environmental sensors after that period.

Mean sap flux (f, cm^3 cm^{-2} h^{-1}, Table 2) from Dec 09 to Aug 10 differed significantly among months, but not between age classes or between sites for each age class. By contrast, estimated sapwood area index did differ between age classes, and was 72% greater in regrowth than mature plots (Fig. 1). However, leaf area index (Fig. 1) was only 35% greater in the regrowth than in the mature sites. As a consequence, the mean plot-level ratio of sapwood area to leaf area was greater, albeit not significantly, in the regrowth (6.8 ± 1.7 vs 5.5 ± 1.4 cm^2 m^{-2}; means $\pm$ 95% CIs, Fig. 1). It should be noted that leaf area index differed greatly between the two mature sites (M1: 1.98 m^2 m^{-2}; M2: 1.24 m^2 m^{-2}), and much less between the two regrowth sites (R1: 2.22 m^2 m^{-2}; R2: 2.13 m^2 m^{-2}).

The nocturnal fraction of diel transpiration, estimated from sap flux by the method of Buckley et al. (2011), was significantly greater in regrowth plots (10.3 ± 0.8%) than in mature plots (7.3 ± 0.8%) (means $\pm$ SE), and also differed significantly between sites for each age class. The time constant for refilling of bole water stores was similar among age classes and sites (2.57 ± 0.16 h; mean $\pm$ SE).

3.2. Evaporative demand and soil moisture

We measured environmental variables for 148 days from December 2009 to June 2010. During this period evaporative demand differed among months (Fig. 2) and was greater in mature than regrowth plots, although the latter difference was significant only during April and May 2010. Soil relative water content at 50 cm differed among months (Fig. 2), and was significantly lower in mature than regrowth plots in all months except May. However, soil relative water content at 20 cm depth did not differ significantly among months or between age classes.

3.3. Effect of environmental variables on sap flux

Multiple linear regression found that evaporative demand was a strong predictor of mean sap flux in outer sensors in all cases ($p < 0.0001$ in all cases; r^2_{adj} ranged from 0.639 to 0.782; df_{error} = 145), but that soil relative water content was not a significant predictor of sap flux in any site ($p > 0.05$). Moderate variance inflation factors (up to 2.0) suggested slight multicollinearity between these two environmental variables, reflecting the tendency for evaporative demand to increase and soil moisture to decline over time after rain events (e.g., Fig. 2). Simple regressions using only soil relative water content as a predictor variable and the ratio of sap flux to evaporative demand (a proxy for crown conductance, intended to isolate the effect of soil moisture on water use) found significant regression slopes in most cases (Table 3). However, coefficients of determination were very low (average and maximum r^2_{adj} = 0.075 and 0.250, respectively) and regression slopes were negative in 4 of 12 cases. These results suggest that soil

moisture does not strongly or consistently control water use in our sites.

3.4. Plot water use

Estimated sap flow at the plot level (Fig. 3) was similar between the two regrowth plots (R1, 2.24 ± 0.28 mm d^{-1}; R2, 2.45 ± 0.25) and between the two mature plots (M1, 0.97 ± 0.19 mm d^{-1}; M2, 1.17 ± 0.46), but was greater in the regrowth than in the mature plots (R, 2.35 ± 0.19 mm d^{-1}; M, 1.07 ± 0.20 mm d^{-1}; means $\pm$ 95% CI). These estimates of water use in the mature plots used observed relationships between inner and total sapwood area (see Appendix A) to weight sap flux estimates from inner and outer probes (no inner probes were in sapwood in the regrowth plots). We estimated upper and lower bounds on mean plot water use in the mature sites by assuming outer probes or inner probes, respectively, were indicative of flow through all sapwood (mean flux was greater in outer than inner probes in all cases); this led to estimates of 0.92 and 1.08 mm d^{-1} for mean water use in the mature plots. Using the upper estimate for water use in the mature plots to be conservative, we conclude that plot water use was at least 1.27 ± 0.28 mm d^{-1} greater in the regrowth plots. Equivalently, water use was approximately 120% greater in the regrowth plots.

These calculations of water use were based on data from a 9-month period (Dec 09–Aug 10), so extrapolation to annual averages may be biased. However, we also have sap flux data from three of the four plots (M1, R1 and R2) spanning an entire year from Sep 09 to Aug 10 (data from Sep to Nov 09 were excluded from our statistical analysis due to missing data from environmental sensors and sap flux sensors at site M2). Plot means of sap flux within that year-long dataset (not shown) were each within 2–6% of the respective means in our 9-month analysis period, suggesting

Table 2
Diameter at breast height (1.3 m, cm), areas of outer and inner sapwood bands (cm^2), and mean sap flux (cm^3 cm^{-2} h^{-1}) during the study period (03 Dec 2009–13 Aug 2010) for outer and inner sensors. Where inner values are not given, this means inner sensors were not in sapwood. M1 and M2 are mature sites; R1 and R2 are regrowth sites.

| Site	Tree	Diameter at 1.3 m	Sapwood area		Sap flux	
			Outer	Inner	Outer	Inner
M1	1	44.0	238.4	42.5	4.40	6.64
M1	2	45.0	220.9	–	5.46	–
M1	3	66.3	371.3	143.2	3.58	3.47
M1	4	52.5	285.9	17.7	6.28	2.90
M1	5	35.8	174.0	–	3.63	–
M1	6	58.5	324.8	46.6	3.96	3.92
Mean ± SE					4.55 ± 0.45	4.23 ± 0.83
M2	1	76.4	428.5	150.1	2.81	6.76
M2	2	48.2	176.1	–	8.07	–
M2	3	53.0	289.0	31.6	8.13	2.73
M2	4	44.1	204.0	–	7.48	–
M2	5	61.3	332.6	115.1	5.43	4.87
Mean ± SE					6.39 ± 1.02	4.79 ± 1.16
R1	1	8.5	53.0	–	5.92	–
R1	2	7.8	44.9	–	8.64	–
R1	3	8.5	39.3	–	8.27	–
R1	4	8.6	62.9	–	7.27	–
R1	5	8.1	45.9	–	7.85	–
Mean ± SE					7.59 ± 0.48	–
R2	1	8.2	31.2	–	4.22	–
R2	2	8.7	50.1	–	6.70	–
R2	3	9.0	44.7	–	7.33	–
R2	4	9.0	37.4	–	5.16	–
R2	5	8.6	48.5	–	6.69	–
Mean ± SE					6.02 ± 0.57	–
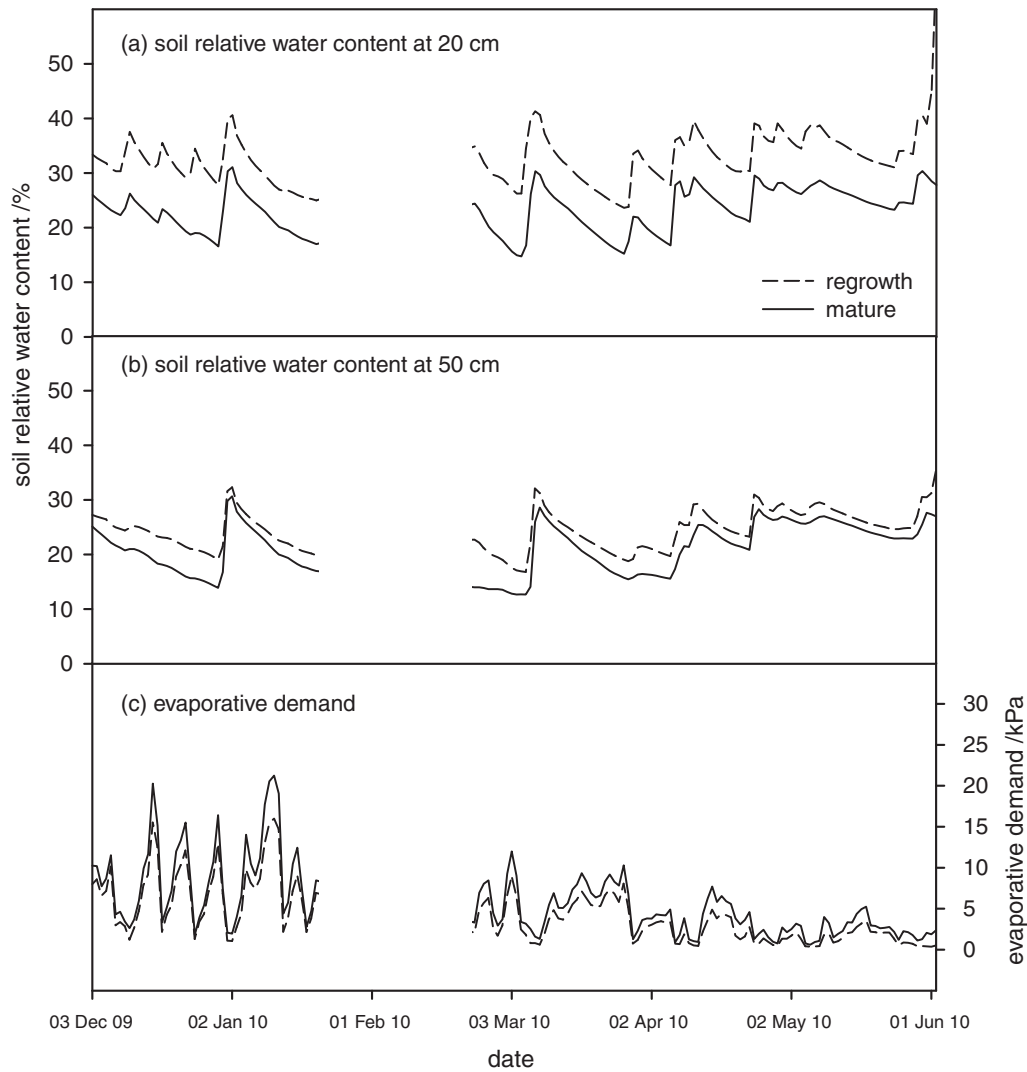
Fig. 1. Soil relative water content and evaporative demand. Daily means of soil relative water content at 20 cm (a) and 50 cm (b), and of evaporative demand (c), averaged for the two regrowth plots (dashed lines) and the two mature plots (solid lines).
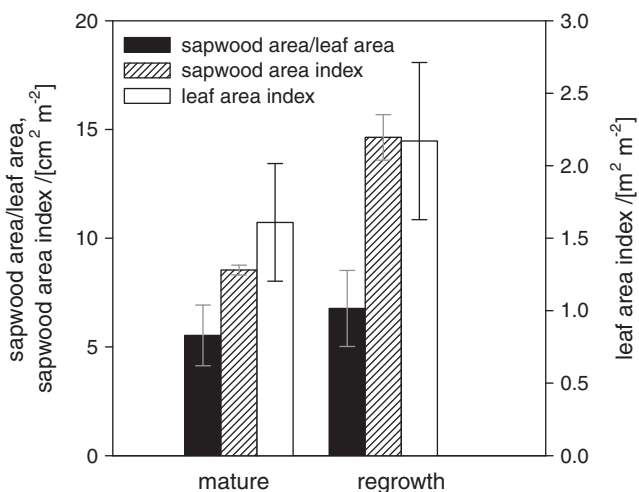

Fig. 2. Leaf area and sapwood area. Leaf area index (right axis, open bars), sapwood area index (grey bars, left axis), and the plot level ratio of sapwood area to leaf area (black bars, left axis) in mature and regrowth plots. Bars are means of two plots. Error bars are 95% confidence intervals.

Table 3

Standardised regression slopes (β) and coefficients of determination (r^2_{adj}) for regressions with the ratio of mean sap flux in outer sensors to evaporative demand as the dependent variable and soil relative water content (measured at 20 or 50 cm depths) as the predictor variable. $df_{error} = 146$.

Site	20 cm		50 cm	
	β	r^2_{adj}	β	r^2_{adj}
M1	−0.569[**]	0.053	−0.238[ns]	0.012
M2	0.400[*]	0.029	0.381[*]	0.034
R1	2.350[***]	0.250	2.490[***]	0.145
R2	0.554[*]	0.042	0.870[*]	0.032

[***] $p < 0.0001$.
[**] $p < 0.005$.
[*] $p < 0.05$.
[ns] Not significant ($p \geqslant 0.05$).

the 9-month period was fully representative of whole-year averages.

Uncertainty in estimated water use was attributable to different factors at each plot. Differences in sap flux among sampled trees contributed 23.1 and 48.8% of the total variance at M1 and M2, respectively, and 17.2 and 29.2% at R1 and R2, respectively. In
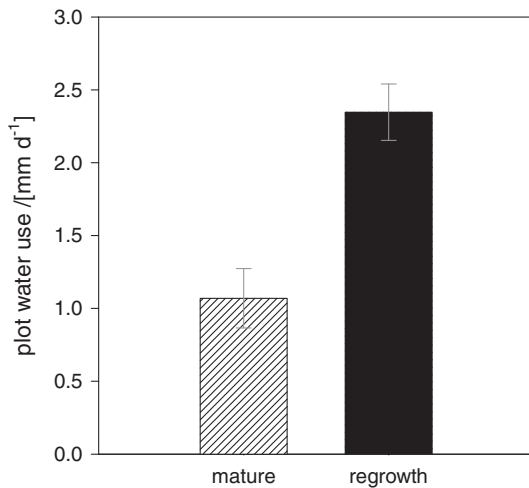
Fig. 3. Plot water use. Plot level water use in mature and regrowth sites (mean of two plots each). Error bars are 95% confidence intervals.

the mature plots, the remaining variance in water use estimates came predominantly from azimuthal variation (which contributed 75.0 and 49.0% at M1 and M2, respectively). Uncertainty in the inference of sapwood area from stem diameter contributed 2.9 and 2.2% of variance at M1 and M2, respectively, and 82.8 and 70.8% at R1 and R2, respectively.

3.5. Leaf physiology (2006–2007 and 2009–2010 campaigns)

Stomatal conductance measured in 2006–2007 was consistently greater in upper-regrowth crowns than in either lower-regrowth crowns or mature crowns (Fig. 4). Stomatal conductance was also greater in the afternoon than in the morning in mature crowns. Photosynthetic capacity did not differ significantly among positions/ages, and neither conductance nor photosynthetic capacity differed between sites for each age class, nor among campaigns. Pre-dawn leaf water potential measured in 2009–2010 at sites M3 and R3 was higher in regrowth than mature trees, but mid-day leaf water potential was similar between age classes (Fig. 6), and did not differ among campaigns.

4. Discussion

We measured water use by young Alpine Ash trees that grew from seed after a stand-replacing fire in 2003, and by mature trees in adjacent plots that survived the fire. Our data suggest plot-level transpiration is about 120% greater, or 1.3 ± 0.3 mm d^{-1} (460 ± 100 mm year^{-1}) greater in the regrowth than in the mature plots, seven years after the 2003 bushfire. Our results are consistent with the rapid initial decline in catchment water yield predicted by the "Kuczera curve" (Kuczera, 1987; Watson et al., 1999). Those predictions were based on measurements of water yield from catchments near Melbourne dominated by Mountain Ash (*E. regnans* F. Muell), a close relative of Alpine Ash that grows at lower elevation sites (e.g., 300–700 m), often with greater rainfall (up to 1800 mm) and on deeper soils. Lane et al. (2010) recorded that mixed-species catchments that included some *E. delegatensis* yielded less water after fire. While we did not measure water yield, our results verify that the biological component of catchment water balance in these high elevation Alpine Ash forests responds quickly following stand-replacing fires. Several sap-flux studies in the Mountain Ash catchments studied by Kuczera (Dunn and Connor, 1993; Vertessy et al., 1995; Vertessy et al., 1997; Vertessy et al., 2001) supported the Kuczera curve projections for stand
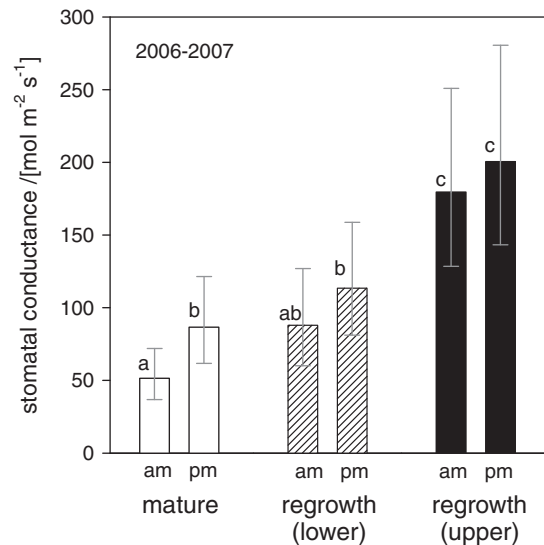

Fig. 4. Stomatal conductance. Stomatal conductance measured in campaigns during 2006 and 2007, in mature crowns and lower and upper regions of regrowth crowns, prior to installation of sap flux sensors in the regrowth trees. LS means ± SEs from ANOVAs, as described in the text. Different letters above bars represent significantly different means ($p < 0.05$, Tukey's LSD post hoc tests).

ages of 15–240 years in age. The present study complements the insights provided by those earlier works by documenting the rapid increase in stand water use, measured seven years after fire.

Our results suggest that the greatest potential to mitigate the effect of fire on water yield through stand thinning may lie in the first decade after fire. This requires reconsideration of the costs and benefits of pre-commercial thinning, to include not only the economic value of the water yield that can be preserved by thinning (Attiwill and Adams, 2008), but also the potential enhancement of wood production in later years if thinning is performed in the first decade of regeneration (Rawlins, 1991; Fagg, 2006). The need for, and potential economic benefits of refined and scientifically-informed
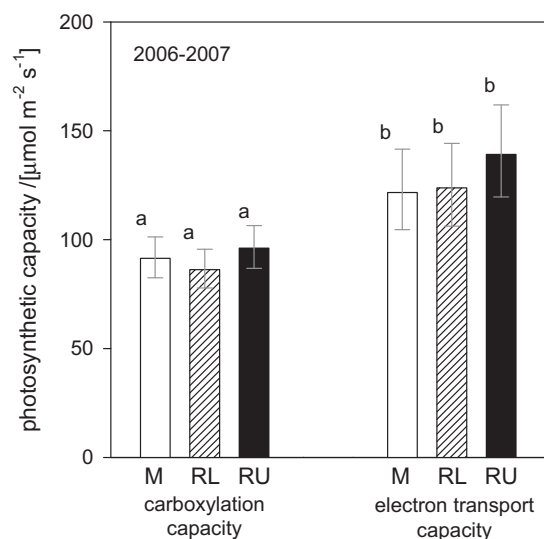

Fig. 5. Photosynthetic capacity. Carboxylation capacity and maximum potential electron transport rate, measured in mature (M), lower regrowth (RL) and upper regrowth (RU) crowns in campaigns during 2006 and 2007, prior to installation of sap flux sensors in the regrowth trees. LS means ± SEs from ANOVAs, as described in the text. Different letters above bars represent significantly different means ($p < 0.05$, Tukey's LSD post hoc tests).

management of ash forests could well increase if fire frequencies increase in the coming century with climate change (Lucas et al., 2007), and as warmer conditions continue to increase water use from these forests (Pfautsch et al., 2010).

Our data suggest a 55% reduction in either leaf area index or sapwood area would be needed to offset greater water use in the regrowth, and potentially maintain water yield. Based on the observed relationship between sapwood area and stem diameter at breast height in the regrowth plots, and on the observed distribution of stem diameters in those plots, this would require removing all stems with a diameter less than approximately 6.8–7.1 cm and a concomitant reduction in stand density by 64%, from around 5900 stems ha^{-1} to 2100 stems ha^{-1}. While such thinning is technically feasible, there are many commercial, social and other ecological issues that need further study (e.g., Attiwill and Adams 2008).

4.1. Why is water use greater in the regrowth?

A clear understanding of the reasons for greater water use in the regrowth, based on measurements of stand properties and both environmental and physiological variables, is useful for the development and testing of process-based models of forest water use. The earlier studies cited above reported similar mean sap flux (flow per unit sapwood area) among stands of differing age (Dunn and Connor, 1993; Vertessy et al., 1997), and our data corroborate those findings. Structurally, the difference in water use with stand age in this study can be attributed to 72% greater sapwood area index in the regrowth plots. Previous work in ash forests yielded similar results: Vertessy et al. (2001); Watson et al. (1999) and Dunn and Connor (1993) found a steep decline in sapwood area with age in E. regnans, as did Roberts et al. (2001) in another ash species, E. sieberi. However, those declines in sapwood area were not matched by commensurate declines in leaf area index. Data given by Watson et al. (1999) suggest overstory leaf area index is approximately 35% greater in 7-year old than 70-year old E. regnans. In the present study, E. delegatensis overstory leaf area index was also 35% greater in the regrowth than in the mature plots. This increased leaf area is not sufficient to explain the greater water use in regrowth as compared to mature stands. Watson et al. (1999) likewise found that the observed changes in leaf area index with stand age in E. regnans were not great enough, when incorporated in a catchment model, to predict observed changes in water yield, and they concluded that water use per unit leaf area must also be greater in younger ash trees.

Our data for E. delegatensis imply that transpiration per unit leaf area, E, was ~61% times greater in the 7-year-old regrowth than in the approximately 71-year-old mature plots. Since evaporative demand (VPD) was also 41% greater in the mature plots, leaf conductance must have been greater still – approximately 128% greater – in the regrowth to account for the extra water use, and boundary layer effects are probably not responsible because the regrowth canopy is much nearer to the ground. Therefore, stomatal conductance was likely much greater in the regrowth than in the mature plots. Limited canopy access prevented extensive direct measurements of conductance to confirm this inference during the study period for which we report sap flux data. However, campaigns in 2006–2007 (when regrowth stems were too small for installation of sap flux sensors) indeed found 175% and 52% greater stomatal conductance in upper and lower regrowth crowns, respectively, than in mature crowns (Fig. 4). Other studies on eucalypts have also found greater stomatal conductance in young trees (Connor et al., 1977; Velikova et al., 2008).

We might question then, why stomatal conductance should be so much greater in the regrowth. Environmental variables may explain part of the difference: soil relative water content at 50 cm was greater in the regrowth, which generally favours enhanced stomatal conductance. However, soil relative water content at 20 cm did not differ between age classes, and we found only very weak relationships between soil moisture and the ratio of sap flux to evaporative demand (a proxy for conductance) across the study period (Table 3). Declining photosynthetic function also can not explain the inferred difference in conductance, because photosynthetic capacity was similar in the two age classes (Fig. 5; measured in 2006–2007). Many previous studies have attributed reduced stomatal conductance in taller trees to the need to sustain leaf water status under burdens of water transport in tall trees (Yoder et al., 1994; Bond and Kavanagh, 1999; Hubbard et al., 1999; Delzon et al., 2004). We found similar mid-day leaf water potential in mature and regrowth trees despite greater pre-dawn leaf water potential in the regrowth (Fig. 6; measured in 2009–2010 at sites M3 and R3, near our sap flux study sites), suggesting that changes in stomatal conductance with age in this species do indeed achieve a degree of hydraulic homeostasis. Anatomical changes may contribute to reduced leaf conductance with age and height in ash, as suggested by a recent study on E. regnans (England and Attiwill, 2006) that found thickened cuticles and waxy deposits blocking stomata in leaves of older, taller trees.

It is intriguing that the community-level ratio of sapwood area to leaf area was slightly greater in the regrowth sites than in the mature sites (Fig. 1). This is consistent with earlier studies on Alpine Ash (Mokany et al., 2003) and Mountain Ash (Watson et al., 1999), which found that sapwood:leaf area ratio declines with increasing age and height in these ash species. However, most species show the opposite trend (McDowell et al., 2002), as predicted by "pipe-model theory" (Shinozaki et al., 1964a,b). That theory suggests that, in order to sustain water transport, sapwood:leaf area ratio should *increase* as trees grow in height to counteract the effects of increased pathlength and gravitational head on xylem pressure gradients. By contrast, a tree growth model based on optimising carbon profits from carbon allocation, DESPOT (Buckley and Roberts, 2006a, b), predicts a shift in carbon allocation away from sapwood production due to the increasing carbon cost of water transport in taller trees. That strategy requires substitution of nitrogen for water as a photosynthetic resource – i.e., increased photosynthetic capacity to compensate for reduced
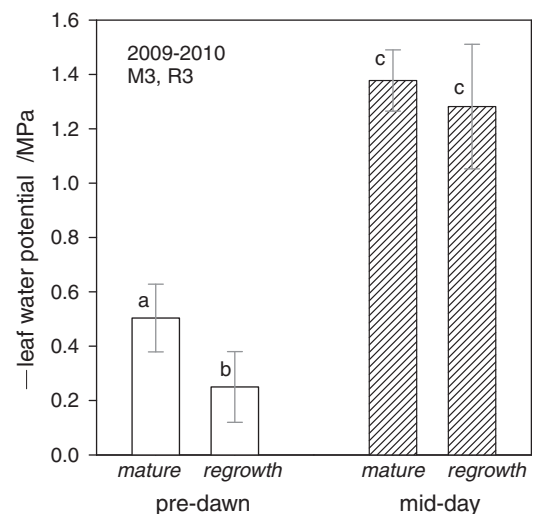

Fig. 6. Leaf water potential. Leaf water potential in mature and regrowth crowns at sites M3 and R3, respectively, measured at predawn and mid-day in three campaigns in 2009–2010. LS means ± SEs from ANOVAs, as described in the text. Different letters represent significantly different means ($p < 0.05$, Tukey's LSD post hoc tests).

stomatal conductance – which, in turn, requires substantial plasticity in the coordination of photosynthetic resource use (Buckley and Roberts, 2006b). The hydraulic effect of reduced sapwood:leaf area ratio may also be offset by an increase in sapwood permeability with height and age, which has in fact been observed in both *E. delegatensis* (Mokany et al., 2003) and *E. regnans* (England and Attiwill, 2007). The occurrence of two such distinct patterns in the coordination of tree growth and leaf gas exchange may reflect a fundamental divergence in the underlying ecological strategies of different species, perhaps due to differences in physiological plasticity at the leaf level, and is worthy of more intensive study. For the present, our data support the view that young eucalypt leaves are adapted to exploit abundant resources in order to maximise carbon gain, whereas adult leaves are more resilient. In general, eucalypts are physiologically plastic in the face of changing resource availability (James and Bell, 2000, 2001).

5. Conclusion

Measurements of sap flux over 9 months in 2009–2010 showed that 7-year-old post-fire regrowth stands of *E. delegatensis* consume 2.2 times more water (an increase of 460 ± 100 mm year^{-1}) than adjacent 71-year old mature stands that survived the 2003 bushfires. This confirms the rapid increase in water use after fire in ash forests suggested by the "Kuczera curve" (1987), and extends the results of earlier studies on post-fire water use by Mountain Ash (*E. regnans*). Changes in leaf area index were insufficient to explain the greater water use and evaporative demand was 41% greater in the mature sites, implying that transpiration and stomatal conductance on a leaf area basis were 1.6 and 2.3 times greater, respectively, in the regrowth. A small part (~3%) of the increased transpiration rate reflected greater nocturnal water use in the regrowth. Similar photosynthetic capacity and mid-day leaf water potential between regrowth and mature trees but lower conductance in the mature trees suggested that the negative impacts of height growth on water transport – increased hydraulic pathlength and gravitational head – are compensated in this species by changes in photosynthetic resource allocation at the leaf level. This is consistent with predictions from optimisation theory (Buckley and Roberts, 2006a,b) and a previous study in this species (Mokany et al., 2003), but it contrasts the prediction that sapwood area per unit leaf area must increase to sustain stomatal conductance, as predicted by "pipe-model theory" (Shinozaki et al., 1964a,b) and supported by data from many northern hemisphere species (McDowell et al., 2002). This knowledge can be used improve predictions of Australian forest water use in a changing climate.

Appendix A. Detailed methods for analysis of sap flux

A.1. Inner vs outer sap flux

Inner probes were not in sapwood in any regrowth trees, but they were in sapwood in 7 of 11 mature trees (Table 2). To address uncertainty in the attribution of different sap flux values to different bands of sapwood in those mature trees, we computed values of water use and its confidence intervals (see below), using three different assumptions: (i) Sap flux measured by outer sensors applies to all sapwood area in each tree. (ii) Sap flux measured by inner sensors applies to all sapwood area in each tree. (iii) Sap flux measured by inner probes applies to a band of sapwood whose area we estimated from total sapwood area based on an observed linear relationship (area of inner band = $0.472 \times$ [total area] $- 111.85$ [for total area > 237], $r^2 = 0.92$, $df_{error} = 7$), and sap flux measured by outer probes applies to all other sapwood.

A.2. Separation of transpiration and refilling

We estimated the nocturnal fraction of diel transpiration by separating the transpiration and bole refilling components of sap flux using a simple flow model; full details and a derivation are given in Buckley et al. (2011). Briefly, the model assumes fluxes across basal sensors and into/out of bole water stores are driven by water potential gradients, which are linked to xylem water content by a constant capacitance. In the model, the ratio of storage resistance and xylem resistance modulates the flows; we assumed a ratio of unity to ensure our estimates of nocturnal transpiration were conservative, as suggested by Buckley et al. (2011). The model also requires estimates for the time constant for refilling bole water stores in the absence of transpiration, which we obtained from sap flow data following Buckley et al. (2011).

A.3. Scaling to the plot level

We estimated average plot-level sap flow in mm d^{-1} from measurements of sap flux in cm^3 cm^{-2} h^{-1} made by individual sensors as follows, for each plot. First, we calculated the mean sap flux for each sensor during the study period, separately for inner and outer sensors. Second, for every stem in the plot, we estimated sapwood area from measured diameter at breast height, using linear regressions for observations in sampled trees. For R1, this equation was [sapwood area in cm^2] = $5.7356 \times$ [diameter in cm] $- 5.9332$, $r^2 = 0.7816$, $df_{error} = 6$, $p = 0.0036$; for R2, the equation was [sapwood area] = $4.9662 \times$ [diameter] $- 7.2177$, $r^2 = 0.9115$, $df_{error} = 10$, $p < 0.0001$. Regression parameters did not differ significantly between M1 and M2, so we pooled those data into a single relationship: [sapwood area] = $11.239 \times$ [diameter] $- 271.21$, $r^2 = 0.9067$, $df_{error} = 9$, $p < 0.0001$. Third, for each stem we multiplied sapwood area by estimates of sap flux from inner or outer sensors, or a weighted sum of both, as described above. Finally, we summed the flows over all stems in each plot and divided by plot area.

We used sap flux data rather than scaled sap flow estimates to compare responses of mature and post-fire regrowth trees to environmental conditions to avoid confounding the latter analysis with uncertainties arising from the scaling process.

A.4. Confidence intervals for plot-level sap flow

We computed 95% confidence intervals (CIs) for estimated values of plot water use as $\pm 1.96 \times$ [standard error for water use], where 1.96 is the normal quantile for $\alpha = 0.95$. We calculated the standard error for water use from the sum of variances in estimated flow for all stems in the plot. Variance for each stem flow estimate was computed as the sum of relative variances for flux and sapwood area estimates. For flux, this included variances both among azimuths and among sampled trees, and for sapwood area, the variance was calculated from the standard deviation of prediction from regressions of sapwood area vs diameter at breast height.

Table C.1. Effect structure of analyses of variance (ANOVAs) used in this study. Each successive effect listed in each row was nested in the nearest effect to the left, except for campaign, which was not nested. For example, age class was nested in month for ANOVAs on sap flux. Treatment levels for "position/age class" were mature, regrowth-upper crown, and regrowth-lower crown. Levels for "time of day" were morning or afternoon for stomatal conductance, and pre-dawn or midday for leaf water potential.

Variable	Effects					
	Month	Age class	Position/age class	Time of day	Site	Campaign
Sap flux	✔	✔			✔	
Evaporative demand	✔	✔				
Soil relative water content	✔	✔				
Time constant for bole refilling		✔			✔	
Nocturnal fraction of diel water use		✔			✔	
Sapwood area index		✔			✔	
Stomatal conductance			✔	✔	✔	✔
Carboxylation capacity			✔		✔	✔
Electron transport capacity			✔		✔	✔
Leaf water potential		✔		✔		✔

Appendix B. Measurement of photosynthetic capacity

To calculate photosynthetic capacity (carboxylation capacity and maximum potential electron transport rate), we measured relationships between leaf net CO_2 assimilation rate and intercellular CO_2 mole fraction under saturating photosynthetic photon flux density (2000 μmol m^{-2} s^{-1}) and leaf temperature 22.2 ± 2.3 °C (mean ± s.d.; temperature varied less than 0.5 °C during each response curve) with a Li-COR 6400 infrared gas analyser (Li-Cor, Lincoln, NE, USA) equipped with an LED light source (Li-Cor) and the standard 2 × 3 cm leaf chamber. Carboxylation capacity was estimated by fitting the RuBP-carboxylation-limited phase of the model of Farquhar et al. (1980) by least-squares regression to 4–5 points at low intercellular CO_2 below a visible transition to RuBP-regeneration limitation. Maximum potential electron transport rate was estimated by applying the values of assimilation rate and intercellular CO_2 measured at saturating CO_2 (ambient $CO_2 \approx 600$ μL L^{-1}) to the RuBP-regeneration-limited phase of the Farquhar model. All estimates were corrected to a common temperature of 25 °C using temperature responses given by Bernacchi et al. (2001) for carboxylation capacity and by de Pury and Farquhar (1997) for electron transport. This procedure was performed for one leaf from one individual per plot in Nov 06 and Jan 07, and from one leaf from each of three individuals per plot in Nov 07. Branches bearing measured leaves had been cut under water with sharp secateurs, with the cut end subsequently kept in water during measurements.

Appendix C. Detailed methods for statistical analyses

C.1. Statistical analysis

We performed analyses of variance (ANOVAs) on ten independent variables, with effect structures as given in Table C.1. We assessed effects of evaporative demand and soil relative water content on sap flux measured by outer sensors using two sets of linear regressions. First, we performed multiple linear regressions on daily means, separately for soil relative water content measured at 20 or 50 cm depth. These regressions invariably showed evaporative demand to be the dominant driver of sap flux ($p < 0.0001$ in all cases), with relative water content being an insignificant predictor in all cases. To isolate the effect of relative water content on sap flux, we performed simple regressions using the ratio of sap flux to evaporative demand (a proxy for canopy conductance) as the dependent variable. Significant fixed effects from ANOVAs reported in the *Results* had p values less than 0.05. The identity and sense of significant treatments were assessed by Tukey's LSD post hoc tests. All statistical comparisons were performed in SAS Enterprise Guide 4.3, running SAS System version 9.2. Quantitative variables were log-transformed to increase normality.

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