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Changes in evapotranspiration components following replacement of *Eucalyptus regnans* with *Acacia* species

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Abstract

Forest species composition may change following a disturbance. This change can affect long term water yield from forested catchments when the replaced and replacement species have different evapotranspiration (ET) rates. Following strip-thinning experiments that removed 50% of the overstorey basal area in several *Eucalyptus regnans* water supply catchments in south eastern Australia, *Acacia* spp. (*Acacia dealbata*, *Acacia melanoxylon*) became the dominant overstorey species in most of the cut strips. More recently, low regeneration of *E. regnans* following wildfires in 2009 may result in mixed *Acacia* and *E. regnans* stands in some catchments. We compared transpiration of *E. regnans* and *Acacia* stands in the uncut and cut strips of a catchment that was strip-thinned in early 1980s (Crotty Creek). We also compared transpiration and throughfall in a mixed *E. regnans* − *A. dealbata* regrowth stand 20 years after clear-fell logging (Road 8). Sap flow was measured for 13 and 6 months at Crotty Creek and Road 8 respectively. In both studies, mean daily sap flow density of *Acacia* spp. was lower than of *E. regnans*. Estimated Leaf Area Index (LAI) of *E. regnans* stands was slightly greater than that of *Acacia* spp. Stomatal conductance (g_c), estimated by inverting the Penman-Monteith equation, differed between the species suggesting species-level physiological differences with *Acacia* being more sensitive to vapour pressure deficit than *E. regnans*. Throughfall measurements at Road 8 indicated interception was slightly higher in *A. dealbata*, but only enough to offset about 13% of the difference in transpiration. Replacement of *E. regnans* by *Acacia* dominated stands may, therefore, decrease catchment ET and increase streamflow.

Keywords: species composition, sap flow, evapotranspiration, *Eucalyptus regnans*, *Acacia dealbata*, stomatal conductance.

1 Introduction

Changes in tree species composition may occur following forest disturbance, such as logging, wildfire, severe drought or outbreak of pests or pathogens (Elliott & Swank, 2008; Ellison et al., 2005; Fensham, Fraser, MacDermott, & Firn, 2015; McKenzie, Gedalof, Peterson, & Mote, 2004). Dominant species may be replaced by co-dominant species due to different survival rates (Cocking, Varner, & Knapp, 2014; Vose & Elliot, 2016) or recruitment/regeneration rates (Benyon & Lane, 2013; Collins, Rhoades, Hubbard, & Battaglia, 2011), while more shade tolerant understorey species can sometimes fill gaps in the canopy (Gray *et al*., 2012). These changes can alter various long term ecosystem functions, including catchment water yield when the replaced and replacement species have different transpiration and interception rates (Brantley, Ford, & Vose, 2013; Ford, Hubbard, & Vose, 2011; Scott, Huxman, Williams, & Goodrich, 2006). As the frequency and severity of forest disturbance are likely to increase with climate change (Allen et al., 2010; Flannigan, Krawchuk, de Groot, Wotton, & Gowman, 2009), understanding the effects of changes in species composition on evapotranspiration (ET) components will improve the modelling of future water yields and management of forested water catchments.

Forest of *Eucalyptus regnans* F. Muell. or *E. delegatensis* R. Baker yield most of the streamflow that supplies drinking water to the city of Melbourne, Australia. These species regenerate after a large-scale disturbance (e.g. wildfire, clear-fell harvesting) as even-aged stands that dominate the overstorey layer of the forest. The impact of the regeneration of *E. regnans* stands on water yield is well understood (Dunn & Connor, 1993; Kuczera, 1987; Langford, 1976; Vertessy, Watson, & O'Sullivan, 2001). However, there have been several instances where shade-tolerant *Acacia* spp. (e.g. *A. dealbata* Link. and *A. melanoxylon* R. Br) have replaced *E. regnans* stands after disturbance (Fairman, Nitschke, & Bennett, 2016). *Acacia* spp. are commonly found as mid-storey or understorey species in undisturbed *E. regnans* forest (Pfautsch, Bleby, Rennenberg, & Adams, 2010; Vertessy, Benyon, O'Sullivan, & Gribben, 1995; Vertessy et al., 2001), although *A. dealbata* can be a substantial component of the overstorey as a subdominant species for at least 15 years (Vertessy et al., 1995). Following strip-thinning experiments in three *E. regnans* catchments in the early 1980s, *Acacia* stands replaced *E. regnans* stands as the dominant overstorey species in most of the cut and regenerated strips (Benyon, 1992; Hawthorne, Lane, Bren, & Sims, 2013). More recently after wildfires in February 2009, the regeneration density of some *E. regnans* stands in two water supply catchments has been unexpectedly low (< 10,000 seedlings ha^{-1}), which may result in the development of mixed or *Acacia*-dominated stands (Benyon & Lane, 2013). Although previous studies have compared sap flow of overstorey *E. regnans* stands and suppressed *Acacia* spp. stands (Pfautsch et al., 2010; Vertessy et al., 1995; Vertessy et al., 2001), sap flow of unsupressed overstorey *Acacia* spp. is unknown. An increased proportion of *Acacia* stands in these catchments may change catchment ET and therefore streamflow.

The objective of this study was to examine the impact of post-disturbance replacement of *E. regnans* stands with *Acacia* spp. stands on ET. We compared transpiration and interception rates of *E. regnans* and *Acacia* spp. growing under the same conditions at two sites (Crotty Creek and Road 8) in Victoria, Australia. We hypothesised that *E. regnans* and *Acacia* dominated stands have different ET rates. Sap flow measurements were obtained to estimate and compare sap flow densities (sap flow per unit sapwood area) of the two species. We found that *E. regnans* and *Acacia* have different radial profiles of sap velocities so we developed a simple sap profile model to integrate sap velocity across the sapwood. Leaf area index (LAI) of the overstorey *E. regnans* and *Acacia* stands at Crotty Creek was derived from Light Detection and Ranging (LiDAR) data, while LAI at Road 8 was estimated from hemispherical photographs. LAI was used in an inverted Penman-Monteith equation to estimate leaf-level stomatal conductance (g_c). Throughfall was measured over a four month period at the Road 8 site and compared in *E. regnans* − *A. dealbata* mixed stands, from which differences in interception were inferred.

2 Materials and methods

2.1 Site description

Measurements were undertaken at two study sites approximately 60 km north east of Melbourne, Australia . Crotty Creek catchment ($37^0$33'S, $145^0$36'E) was subjected to strip-thinning from 1980 to 1985 and consisted of 35 m wide alternating strips of *E. regnans* stands and regrowth stands with *Acacia* spp. overstorey, approximately 55 m and 20 m tall respectively. The second site, located on the northeast side of Road 8, just outside of Maroondah catchment ($37^0$37'S, $145^0$39'E), contained a mixed stand of *E. regnans* and *A. dealbata* regenerated following clear-fell harvesting in 1996. The tree heights at Road 8 were not measured accurately, but co-dominant trees of both species were visually of similar height to each other.

2.1.1 Crotty Creek

The 122 ha Crotty Creek catchment is located on the northern slopes of the Great Dividing Range. The elevation ranges from 685 m to 815 m. The climate is temperate (monthly mean maxima and minima of 23 ^{0}C and 11 ^{0}C in January and 9 ^{0}C and 4 ^{0}C in July) and rainy (mean annual rainfall of 1822 mm for the period of 1977 to 1996). The soils are deep, well drained brown or red ferrosols with a high clay content (60 - 80%), very friable consistency and acid throughout the profile. The surface soils are highly permeable, loamy structures, with high moisture holding capacity. Soil depth is estimated to be 4 - 5 m, with hydraulic conductivity of 1.6 m day^{-1} for the subsoil layer (Davis, Vertessy, & Silberstein, 1999).

Strip-thinning was carried out at Crotty Creek in several stages from the summer of 1979/1980 to the summer of 1985/1986: 50% of the total basal area was removed in alternating strips 35 m wide, which resulted in uncut and cut strips parallel to the contours. Before thinning, the catchment was dominated by 1939 regrowth *E. regnans* stands. Common understorey species included *A. melanoxylon*, *A. dealbata*, *Pomaderris aspera*, *Hedycarya* *angustifolia*, *Olearia argophylla*, *Zieria arborescens*, *Correa lawrenciana* and *Dicksonia antarctica*. In 2007, *Acacia* spp. and *Dicksonia antarctica* made up approximately 43% and 30% of the basal area of the cut strips respectively (Tran, 2007).

2.1.2 Road 8

Road 8 is located near the north-eastern boundary of Maroondah catchment, approximately 10 km southeast of Crotty Creek. The study plots were located on a gently sloping easterly aspect on the northeast side of Road 8, just outside of Maroondah catchment, on the northern slopes of the Great Dividing Range at 550 m elevation. Climate and soil, although not studied in detail, are likely to be similar to Crotty Creek.

2.2 Weather data collection

At Crotty Creek, an automatic weather station (Micropower data logger, Tain Electronics, Victoria, Australia) recorded solar radiation, rainfall, temperature, wind speed and relative humidity at a height of 3.5 m every half hour from December 2009. It was located in a logging coupe east of the catchment ($37^0$32.8'S, $145^0$35.3'E). Vapour pressure deficit (VPD) was calculated from temperature and relative humidity. There are several gaps in data due to logger failure in February 2010 and May to August 2010. The first summer of the measurement period coincided with the end of a long drought that affected south eastern Australia from the mid-1990s to 2009 (Verdon-Kidd & Kiem, 2009), while the second summer coincided with the start of a ‘La Nina’ event so it was unusually wet and humid.

At Road 8, similar climatic variables were also recorded every half hour at an automatic weather station located about 200 m west of the measurement plots. It was noted that the weather station may be partly shaded by the canopy of a nearby *E. regnans* tree so rainfall and solar radiation may have been underestimated.

2.3 Sampling plots

2.3.1 Crotty Creek

Sap flow measurements were conducted in two pairs of plots, each consisting of one plot in the uncut strip and a second plot in the adjacent cut strip. The first plot pair (P1U, P1C) was located in the southern part of the catchment, with east − west strip orientation. Each plot covered an area of 15 x 15 m. The second pair was located in the eastern part of the catchment, where *A. dealbata* occurs both as an overstorey species in the cut strip (P2C) and as an understorey species in the adjacent uncut strip (P2U), with northeast − southwest strip orientation. P2C covered an area of 15 x 15 m, while P2U covered an area of 15 x 20 m to include some *Acacia* understorey trees. The *E. regnans* stands in the uncut strips were approximately 70 years old (1939 regrowth), while the *Acacia* stands in the cut strips were approximately 24 – 29 years old (post-thinning).

Table 1 provides information on topography, dominant species, basal area and sapwood area of the overstorey vegetation in the four sample plots. In Plot P2U, understorey *A. dealbata* contributed 47% to the total understorey basal area, while *P. aspera* made up the rest of the woody understorey.

2.3.2 Road 8

The mixed *E. regnans* − A. *dealbata* stand at the second site tended to contain distinct clumps of each species. To compare sap flow rates in almost pure stands, three small plots were established in each of three clumps of both species within a 60 m x 60 m area. These sap flow sample plots were circular, each containing five dominant trees of one species, with no more than one dominant tree of the other species, although the eucalypt plots also contained some sub-dominant or supressed *A. dealbata*. Plot size was determined by the distance of the sixth dominant tree from the plot centre. In addition, 9 circular inventory plots, 15 m in diameter, were established on a 3 x 3 grid within the 60 m x 60 m area and the species and diameters of all trees in each of these plots recorded. Table 2 gives details of the stocking density, mean stem diameter and estimates of sapwood area in each sap flow sample plot and in the nine inventory plots.

2.4 Sap flow measurements

2.4.1 Crotty Creek

The compensation heat pulse (CHP) method (Dunn & Connor, 1993; Green, 1988; Hatton, Moore, & Reece, 1995) was used to measure sap flow in individual trees from 16 December 2009 until 31 January 2011. The CHP probes were installed in parallel holes drilled radially into the stem. Each set of probes consisted of a heater probe and two temperature sensor probes. One temperature sensor probe was installed 10 mm above the heater probe, while the other was installed 5 mm below the heater probe. A short heat pulse was emitted every half hour. The time taken for both temperature sensors to register equal temperature was used to calculate heat pulse velocity. The heat pulse velocity was corrected for probe misalignment and wounding (Swanson & Whitfield, 1981), then converted to sap velocity (v, mm hr^{-1}) using the volume fractions of water and wood in the sapwood measured in the increment core samples.

Most sample trees were implanted with four sets of probes, but eight sets were used in the largest *E. regnans* tree and only two sets were used in the two smallest *Acacia* trees (see Table 3). The probes were placed at different depths below the cambium and quadrants around the stems, which enabled the complete radial profile of sap velocity to be sampled. Heat pulse velocities were logged using CR1000 and CR10X data loggers (Campbell Scientific Inc., Logan, UT, USA).

The compensation heat pulse technique has difficulty in differentiating low sap flow from zero sap flow (Becker, 1998). Hence, a threshold sap velocity was determined for each probe at 90% probability of exceedance of sap velocity recorded during a period when the sap flow is likely to be zero, such as when the night-time VPD was close to zero (Benyon, 1999). The threshold sap velocity was calculated for each month of the measurement period, except for the periods when the half-hour VPD data were unavailable. The sap velocity below the threshold value was set to zero. This adjustment also ensured that night time sap flow could be attributed to actual transpiration driven by the evaporative demand (non-zero VPD) or to the refilling of water in the stem and branches that may have been depleted during the daytime. Missing half-hour sap velocities were estimated with linear interpolation when the period of missing data was less than two hours or the change in sap velocities preceding and following the gap was very small (i.e. slow moving sap).

Sapwood thickness (cm) was determined by extracting a number of 5-mm diameter increment cores (4-8 per tree depending on tree size) at breast height. The core samples of *E. regnans* were stained with 1% methyl orange solution to enhance the colour change that identified the sapwood – heartwood boundary, while the core samples of *Acacia* showed the sapwood – heartwood boundary clearly without staining. The mean sapwood thickness obtained from the core samples, diameter at breast height (dbh) and bark thickness were used to calculate the sapwood area of each tree (cm^2).

Tree diameter and sapwood thickness were measured in *E. regnans*, *A. dealbata* and *A. melanoxylon* trees of various sizes inside and outside the plots. A relationship between dbh and sapwood area was established for each vegetation group (*E. regnans* overstorey, *Acacia* overstorey and *Acacia* understorey), which was used to estimate stand sapwood area for that group in the plots based on a census of dbhs.

2.4.2 Road 8

From mid October 2015 to early April 2016, the heat ratio (HR) method (Burgess et al., 2001) was used to measure sap velocities at 1.3 m height in the 15 *A. dealbata* and in 14 of the 15 (the logger in the 15th tree failed) *E. regnans* sample trees. One HR data logger (ITC

International, Armidale, Australia) per tree measured heat pulse velocities at two depths every 30 minutes. The upstream and downstream sensors were placed 5 mm from the heater. Wound corrections, based on wounds measured at the end of the study, and analytical procedures followed Burgess *et al*. (2001). Zero flow values were determined by cutting the sapwood a few cm below the probes and continuing measurements for a further 24 hours at the end of the study.

As the 35 mm HR probes were not always long enough to reach the inner sapwood, CHP sensors were installed at 29 to 37 mm depth in the sapwood of the seven *E. regnans* and two *A. dealbata* trees with the thickest sapwood. About half way through the study, sap flow probes in *A. dealbata* trees in Plot A1 and A3 were moved 0.5 cm closer to the cambium (shallower) in January 2016. After this shift, mean daily sap velocities at the deeper sensor position were estimated based on a linear relationship between previous measurements and mean daily sap velocities at a similar depth from sample trees at Plot A2.

Sapwood thickness was measured at four points around the circumference of each tree and in additional smaller trees in each of the six sap flow sample plots, giving sapwood thickness measurements in 23 *E. regnans* and 35 *A. dealbata* trees. Regression relationships between tree mean sapwood thickness and dbh were applied to all trees in the nine larger inventory plots and stand sapwood area was derived by summing estimates of individual tree sapwood areas.

2.5 Estimating sap flow and transpiration

To obtain the volume of sap flowing through the xylem tissue of each tree, sap velocities at various depths need to be integrated radially from the heartwood to cambium and circumferentially around the bole (Berdanier, Miniat, & Clark, 2016; Caylor & Dragoni, 2009; Edwards & Warwick, 1984):

$$Q = \int_{Rin}^{Rout} 2\pi(r - x)v(x)dx \qquad \text{(Equation 1)}$$

where Q is sap flow, r is radius of the tree, x is the depth from cambium, $v(x)$ is sap velocity as a function of radial depth (sap profile), R_{in} and R_{out} is the radii at heartwood and cambium respectively. The weighted average method (Hatton, Catchpole, & Vertessy, 1990) approximates the radial sap profile with a weighted mean velocity, where the weights are based on proportional area of sapwood centred at probe locations along the radial profile. This method requires sap velocities being sampled at equal areas and roughly uniform across the radial profile. Although the radial sap profile for *E. regnans* in our study appeared to satisfy these requirements, sap velocity of *Acacia* decreased rapidly with depth so the weighted average method would overestimate the whole tree sap flow. Thus, we needed a robust method that can accommodate the different radial sap profiles of *E. regnans* and *Acacia* spp.

Several studies have modelled continuous radial sap profile that decays with depth into the heartwood using modified probability functions (Bell et al., 2015; Berdanier et al., 2016; Caylor & Dragoni, 2009; Gebauer, Horna, & Leuschner, 2008). As we have measured sap velocities at multiple depths (i.e. 2- 4) for each tree, we adopted a simpler model that integrated the radial sap profile linearly between measurement points and sum sap volumes from those segments. This avoided the need to determine the shape of the radial sap profile in the absence of a large number of sap velocity samples. Equation 1 was solved analytically for each segment:

$$Q = \frac{\pi}{3}\{r_{out}^2(2v_{out} + v_{in}) - r_{in}^2(2v_{in} + v_{out}) + r_{in}r_{out}(v_{in} - v_{out})\} \qquad \text{(Equation 2)}$$

where Q is sap flow, r_{in} and r_{out} are the radii of the inner and outer points of the segment, v_{in} and v_{out} are the velocities at the inner and outer points of each segment. Sap velocity at the sapwood − hardwood boundary was assumed to be zero. Meanwhile, sap velocity measured at the outer most probe was assumed to continue to the cambium − sapwood boundary as sap velocities were detected very close to this boundary in the *Acacia* trees.

Daily sap flow (Q, kg day^{-1}) of each sample tree was obtained by averaging half-hour sapflow and multiplying it by 24 hours. Daily sap flow density (J_s, m^3 m^{-2} day^{-1}) was calculated for each tree by dividing the daily sap flow by its sapwood area. Missing J_s of a sample tree at Crotty Creek was gap-filled based on a linear relationship of J_s between that tree and another tree of the same species in the same plot when coefficient of correlation (R^2) is greater than 0.9. Mean stand J_s for each vegetation group was multiplied by the total sapwood area for that vegetation group in all plots, then divided by the corresponding total plot area to obtain transpiration (E_t) in mm day^{-1}.

2.6 LAI estimates

LAI estimates for Crotty Creek were derived from LiDAR data. The data were acquired on 26th August 2007 with a discrete-return sensor. The sensor recorded up to four data points for each laser pulse. LiDAR system configuration and flight detail are summarised in Table 4. The estimation of effective LAI at a fixed height from LiDAR-derived gap fraction is as follows (Lovell, 2003; Riano, Valladares, Condes, & Chuvieco, 2004):

$$L_h = -\frac{1}{k} ln(P_h) = -\frac{1}{k} ln(1 - fCover_h) == -\frac{1}{k} ln\left(1 - \frac{N_{v,h}}{N_t}\right) \qquad \text{(Equation 3)}$$

where L_h is effective leaf area index above height h, k is extinction coefficient, P_h is gap fraction at height h, $fCover_h$ is the vegetation cover at height h, $N_{v,h}$ is the number of vegetation hits above height h and N_t is the total number of hits. An extinction coefficient of 0.5 that represents random foliage distribution has been assumed in this study. The mean gap fraction was extracted from a circular area with 15 m radius around the centre of each sampling plot. LiDAR-derived canopy height profiles of Crotty Creek have shown that the height of the overstorey *E. regnans* stands is greater than 30 m, while the height of the overstorey *Acacia* stands is between 3 and 30 m (Hawthorne et al., 2013). Thus, the effective LAI for the overstorey vegetation were estimated at above 30 m and at 3 - 30 m for the *E. regnans* and *Acacia* stands respectively.

LAI estimates at Road 8 were derived from hemispherical photographs using the Hemisview software (Rich P.M., 1999). The photographs were obtained from the centre of each sample plot.

2.7 Stomatal conductance

To compare species-level canopy conductance, stomatal conductance (g_c, mm s^{-1}) was derived from the LAI and E_t measurements by inverting the modified Penman-Monteith equation (Jarvis & McNaughton, 1986):

$$g_c = \frac{\gamma \lambda E_L g_a}{\Delta R_n + k\rho C_p D g_a - \lambda(\Delta + \gamma) E_L} \qquad \text{(Equation 4)}$$

where g_c is stomatal conductance (mm s^{-1}), γ is psychrometric constant (0.066 kPa C^{-1}), λ is latent heat of evaporation of water (2465 kJ kg^{-1}), E_L is stand mean daily transpiration per leaf area index (mm d^{-1}), g_a is aerodynamic conductance (mm s^{-1}), Δ is the slope of saturation vapour pressure – temperature relationship (kPa C^{-1}), R_n is net radiation (kJ m^{-2} d^{-1}), k is a constant of 86.4 to convert mm s^{-1} to m d^{-1}, ρ is density of air (1.225 kg m^{-3}), C_p is specific heat of air at constant pressure (1.01 kJ kg^{-1} C^{-1}), and D is mean daytime VPD (kPa).

The daily transpiration used for analysis at both study sites was selected during dry days when the average daytime VPD was greater than zero. The aerodynamic conductance (g_a) for forest was assumed to be 0.2 m s^{-1} (Kelliher, 1993), which was used to calculate g_c for the overstorey *E. regnans* and *Acacia* stands. At Crotty Creek, the g_c estimates were based on an assumption that the same g_a, average radiation and average VPD applied to both vegetation groups despite their difference in canopy heights. To test the sensitivity of g_c estimates to the potential variation in climatic variables, the following scenarios were applied: (1) similar g_a, radiation and VPD for the *E. regnans* and *Acacia* stands, (2) lower g_a of 0.1 m s^{-1} in the *Acacia* stands, (3) 50% reduction of the radiation and 25% reduction of the VPD in the

Acacia stands. The second scenario tested the impact of greater aerodynamic resistance in the *Acacia* stands, while the third scenario represented the effects of possible shading of the *Acacia* stands from the adjacent *E. regnans* stands.

2.8 Throughfall

At Road 8, throughfall was determined for each species between November 2015 and March 2016 by placing 11 throughfall collectors (1.2 m x 0.14 m) per species randomly among the three sap flow sample plots. Each collector drained into a closed 30 L container, emptied approximately monthly.

2.9 Statistical analysis

Repeated two-factor ANOVA was used to test variation in mean daily *Js* amongst vegetation group (e.g. overstorey *E. regnans*, overstorey *Acacia* and understorey *Acacia*) and plots with sample tree as the repeated factor. Two-factor ANOVA was used to examine differences in mean daily g_c between scenarios at Crotty Creek, and the effects of maximum VPD and species on mean daily g_c. Paired student's t-test was used to compare mean E_t of overstorey *E. regnans* and *Acacia* stands. Tukey's post hoc HSD was used to separate levels of variables. All statistical analysis was performed with R version 3.2.2 (The R Foundation for Statistical Computing, Vienna, Austria).

3 Results

3.1 Radial sap profile and sap flux

Comparison of mean sap velocities at different depths suggest that *E. regnans* and *Acacia* have different radial sap profiles (Figure 1). For the *E. regnans* trees at Crotty Creek, mean sap velocities in the middle of sapwood were generally greater than those in the inner or outer-most probes. This pattern was less obvious in the *E. regnans* trees at Road 8 because sap velocities were only measured at two points along the sapwood width with the HR probes. However, CHP probes were installed in six of *E. regnans* sample trees at Road 8 to measure sap velocities deeper into the sapwood (> 79% sapwood width). The mean velocities from four out of six trees installed with CHP probes at Road 8 were lower than the velocities measured by HR probes at shallower positions (data not shown), which suggests that sap velocities decreased towards the heartwood in these trees. For most of the *Acacia* trees at both study sites, sap velocities reached their maximum near the cambium then decreased rapidly towards the heartwood. Although sap velocities were recorded by the outer sensors of HR probes in *Acacia* trees after the probes were moved outward in January 2016, these data were excluded in this comparison as the locations of these sensors were very near or beyond the estimated cambium − sapwood boundary.

Figure 1. Mean sap velocity of *E. regnans* (solid triangle) and overstorey *Acacia* (solid circle) sample trees at Crotty Creek and Road 8 as a function of fraction of sapwood width (probe depth divided by sapwood width). The same colour indicates trees from the same plot.

These sap velocity profiles were used to formulate the two boundary conditions for the integration of sap velocities along the sapwood width in the linear interpolation method.

Firstly, sap velocity below the cambium was assumed to be similar to sap velocity measured at the outer-most probe. This translated to low sap velocities for most *E. regnans* trees and high sap velocities for *Acacia* trees at the cambium − sapwood boundary. Secondly, sap velocity at the sapwood − heartwood boundary was assumed to be zero.

The weighted average method (WA) generally produced greater Q estimates than the linear interpolation (LI) method. For example, Q_{WA} of *E. regnans* trees was on average 3-17% greater than Q_{LI} at Crotty Creek, while the average difference in Q of *Acacia* trees was 1-15% between the two methods. The largest difference in Q between methods occurred when the deepest part of the sapwood (e.g. 70 - 100% of sapwood width) was not sampled by the probes, or when a large difference in sap velocities was recorded by neighbouring probes at successive depths.

3.2 Comparison of sap flux density and transpiration between *E. regnans* and *Acacia*

Mean daily J_s varied with available energy, represented by radiation and maximum VPD (VPD_{max}) at each site and measurement period (Figure 2). J_s increased through the warmer months, then gradually decreasing in the cooler months. Overstorey *E. regnans* stands had greater mean daily J_s than overstorey *Acacia* stands. Climatic input varied between measurement periods. The average daily radiation during the warmer periods (i.e. December - March) of 2009/2010, 2010/2011 and 2015/2016 were 19.1, 17.2 and 16.2 MJ day^{-1} respectively. The average VPD_{max} was 1.68, 1.28 and 1.91 kPa for the three periods. Rainfall total was not compared between sites due to missing daily data at Crotty Creek. However, rainfall total obtained from a gridded climate database (SILO, Department of Science, Information Technology and Innovation, Queensland, Australia) for the location of Crotty Creek yielded 372, 587 and 306 mm for the three periods, suggesting the summer of 2015/2016 was the driest.

Figure 2. Mean daily sap flow density of overstorey *E. regnans* (Eos), overstorey *Acacia* (Aos) and understorey *Acacia* (Aus); daily solar radiation, rainfall and maximum VPD at Crotty Creek (left panel) from January 2010 to February 2011 and Road 8 (right panel) from November 2015 to April 2016.

We compared mean daily J_s over the warmer months (December to March) between vegetation groups, using days when data from all sample trees were available (Table 5). At Crotty Creek, mean J_s of overstorey *E. regnans* (2.33 m^3 m^{-2} day^{-1}) was 16% greater than mean J_s of overstorey *Acacia* (2.02 m^3 m^{-2} d^{-1}) and approximately double the mean J_s of understorey *Acacia* (1.12 m^3 m^{-2} d^{-1}). The difference in mean J_s between vegetation groups was statistically significant, but plot had no significant effect (repeated two-factor ANOVA, group effect: $F_{2,9} = 6.43$, $p = 0.02$; plot effect: $F_{2,9} = 0.24$, $p > 0.05$). At Road 8, *E. regnans* had greater mean J_s than *A. dealbata* (3.08 and 1.80 m^3 m^{-2} day^{-1} respectively). The difference in mean J_s between species was statistically significant, while plot effect was not significant (repeated two-factor ANOVA, species effect: $F_{1,23} = 6.96$, $p = 0.01$, plot effect: $F_{4,23} = 0.69$, $p > 0.05$). Variation between sample trees of the same species at both study sites was statistically significant.

Mean daily E_t at Crotty Creek from January to December 2010 were 1.56 mm d^{-1} and 1.13 mm d^{-1} for overstorey *E. regnans* and *Acacia* stands respectively (Table 5), with estimated annual total E_t for both vegetation groups of 534 and 347 mm. At Road 8, mean daily E_t of overstorey *E. regnans* and *Acacia* over the 6-month measurement period were 2.64 mm d^{-1} and 1.45 mm d^{-1} respectively, with total E_t for both species of 465 mm and 252 mm. The difference in mean E_t between species was statistically significant (Student's paired t-test, $p < 0.05$).

3.3 Overstorey LAI and stomatal conductance

At Crotty Creek, effective LAI of the dominant overstorey species was estimated from LiDAR data in each sample plot. The difference in the mean effective LAI between overstorey *E. regnans* (1.77) and *Acacia* (1.55) stands in the sample plots was small (Table 6). Mean effective LAI of the two vegetation groups was also similar at Road 8 (2.83 and 2.55). There was greater variation in LAI between plots of the same species than variation between species at both study sites.

Effective LAI and mean daily plot E_t were used to calculate g_c for the overstorey *E. regnans* and *Acacia* stands (Equation 4). Assuming similar climatic variables applied to both stands at Crotty Creek (first scenario), the mean g_c values of *E. regnans* and *Acacia* stands were 2.41 mm s^{-1} and 1.90 mm s^{-1} respectively (Figure 3). The differences in mean g_c between vegetation groups under various scenarios were significant (repeated one-factor ANOVA; scenario: $F_{3,306} = 314$, $p < 0.01$) . However, *Acacia* could have greater g_c than *E. regnans* if the *Acacia* stands were exposed to lower radiation and VPD due to shading from the neighbouring *E. regnans* stands.

Figure 3. Mean daily stomatal conductance (g_c) of the overstorey *E. regnans* and *Acacia* stands at Crotty Creek for a range of scenarios: similar climatic parameters in *E. regnans* and *Acacia* stands, g_a of 0.1 m s^{-1} in *Acacia* stands, 50% radiation and 75% VPD in *Acacia* stands. Letters denote statistically significant difference ($p < 0.05$) between groups.

Mean daily g_c decreased with increasing VPD_{max} (Figure 4). Under the same VPD_{max}, g_c of *Acacia* was generally lower than g_c of *E. regnans* at both study sites. Greater ranges of g_c and VPD_{max} were captured in the Road 8 data than the Crotty Creek data. VPD_{max} and species had significant effects on g_c at Crotty Creek, but interaction between the two factors was not significant (two-factor ANOVA; VPD_{max} effect: $F_{1,202} = 150$, $p < 0.01$; species effect: $F_{1,202} = 62.7$, $p < 0.01$; interaction: $F_{1,202} = 3.49$, $p = 0.06$). Meanwhile, the interaction between daily VPD_{max} and species had a significant effect on g_c at Road 8 (two-factor ANOVA; VPD_{max} effect: $F_{1,226} = 118$, $p < 0.01$; species effect: $F_{1,226} = 16.4$, $p < 0.01$; interaction: $F_{1,226} = 9.74$, $p < 0.01$).

Figure 4. Variation in mean daily stomatal conductance (g_c) of the overstorey *E. regnans* and *Acacia* stands against daily maximum VPD at Crotty Creek and Road 8.

3.4 Throughfall

The measurements of throughfall at Road 8 indicated throughfall was statistically significantly lower ($p<0.01$) under *A. dealbata*.Between November 2015 and March 2016, throughfall collected under *E. regnans* totalled 246 mm compared with only 219 mm under *A. dealbata*. Although stem flow was not measured, the results indicate interception loss was approximately 11% higher from *A. dealbata* than from *E. regnans*.

4 Discussion

4.1 Comparison of ET components between species

The difference in mean daily J_s between the overstorey *E. regnans* and *Acacia* stands (Figure 2, Table 5) suggest there may be species-level physiological differences that control their transpiration. Based on modelling of g_c with LAI and E_t estimates, overstorey *Acacia* spp. stands had lower mean daily g_c than *E. regnans* stands (Figure 3, Figure 4). A difference in g_c between other eucalyptus and acacia species has also been observed in a mixed plantation of *E. globulus* Labill. and *A. mearnsii* de Wildeman (Forrester, Theiveyanathan, Collopy, & Marcar, 2010). Thus, the replacement of overstorey *E. regnans* with *Acacia* stands with similar stand sapwood area is likely to reduce catchment E_t.

At Road 8, canopy interception, inferred from throughfall measurements, was greater in *A. dealbata* stands than in *E. regnans* stands despite slightly lower estimated LAI. This may be due to a difference in the morphology and arrangement of foliage in the two species. *E.*

regnans trees have large, smooth, flat leaves that hang vertically, which would facilitate throughfall, whereas *A. dealbata* leaves are much smaller and tend to be arranged in dense clumps more horizontally so may trap and evaporate more rainfall. Higher throughfall of 27 mm under *E. regnans* stands is much less than the 208 mm higher transpiration from *E. regnans* stands over the same period. The likely lower interception by *E. regnans* does not nearly offset its higher transpiration: the extra throughfall accounting for only 13% of the higher transpiration from *E. regnans*.

The change in overstorey composition may also affect water use of shrub and fern species found in *E. regnans* forests, such as *Dicksonia antarctica*. Increased rainfall interception under *Acacia* overstorey may decrease moisture availability for understorey vegetation, while sub-canopy light transmission that influences photosynthesis rate may differ under the two overstorey species. For example, *D. antarctica* harvests rainfall through its funnel-shape fronds (Hunt, Davidson, Unwin, & Close, 2002) and it is more vulnerable to drought stress under moderate than high light regimes (Volkova, Bennett, Merchant, & Tausz, 2010). Although g_c of *D. antartica* may be relatively low (Volkova et al., 2010) compared to g_c of overstorey species, its basal area is a significant component of understorey basal area at Crotty Creek. Measurements of sub-canopy light availability and soil moisture may help estimate the potential change in understorey E_t, which will improve stand ET estimate.

4.2 Uncertainties and variation in transpiration estimates

Reliable estimates of whole-tree *Q* require the integration of sap velocity along the sapwood width. Although the weighted average method has been shown to generate less error than fitting a polynomial to the observed sap velocities (Hatton et al., 1990), this method would introduce positive bias when the radial sap profile varies greatly along the sapwood width as we have observed in *Acacia* spp. Thus, the use of a continuous linear function is a compromise between fitting a complex function and assuming step-changes in sap velocity between probe positions. However, there were several uncertainties in our *Q* estimates. Sap velocities at cambium - sapwood and sapwood - heartwood boundaries were not measured so we assumed the former to be similar to the velocity measured at the outer-most probe and the latter to be zero. The spacing of the two sensors in each HR probe is such that the maximum (minimum) sap velocity may not have been captured, which would result in an underestimation (overestimation) of *Q* as sap velocity was assumed to vary linearly between the two measurements. This risk was greater for *E. regnans* trees as its maximum sap velocity appeared to occur between 30 and 80% into the sapwood (see Figure 1). Employing the weighted average method will not minimise this risk as the average sap velocity would be derived from two observations. We recommend that radial sap profile models for various *Eucalyptus* and *Acacia* species to be developed further in order to reduce uncertainties in *Q* estimates, especially when the number of measurements is limited.

Variation in mean daily J_s between plots of the same species was smaller (not significant) than variation between sample trees. However, this variation did not appear to be related to the variation of sapwood area or LAI. Meanwhile, the difference in mean J_s of overstorey and understorey *Acacia* stands at Crotty Creek suggests that water use of *Acacia* may be sensitive to micro-climatic variables (e.g. radiation, relative humidity, VPD). In estimating stand E_t at Road 8, we have assumed that trees from the same species had the same J_s whether they occur as dominant or less dominant in the mixed stands as we did not measure sap flow of the less dominant trees. Actual water use of the more suppressed trees, such as *A. dealbata* trees in Plot E1 - E3, could have been more limited than the water use of that species when they dominated the stands as dominant trees may have better access to soil water storage and light (less shading). Further study that measures climatic variables at multiple canopy heights may better explain the coupling between water use and atmospheric demand for both dominant and suppressed tree species in mixed stands, while soil moisture measurements may indicate soil water availability to overstorey, understorey or suppressed trees.

The discrepancy in *Js* of *E.regnans* between Road 8 and Crotty Creek appeared to be greater than the discrepancy in J_s of *Acacia* between sites (Table 5). This may be attributed to several factors. The two studies were conducted during periods of different climatic inputs (Figure 2), with the summer of 2015/2016 being dryer with lower humidity than the summers of 2009/2010 and 2010/2011. As *E. regnans* maintains greater stomatal conductance than *Acacia* at high VPD (Figure 4), similar energy demand to the summer of 2015/2016 could have resulted in greater mean J_s of *E. regnans* being observed at Crotty Creek, without a large change in mean J_s of *Acacia*. Mean summer J_s at Crotty Creek may have also been underestimated due to J_s data being unavailable until 28 January 2010, thus excluding the early summer period when greater daily sap flow rate is likely to occur. Lastly, mean J_s of three *E. regnans* sample trees at Road 8 (E1 T3, E2 T2 and E2 T3) over the summer period ranged between 5.4 and 6.3 m^3 m^{-2} day^{-1}, while mean J_s of the other 11 trees over the same period ranged between 1.64 and 3.31 m^3 m^{-2} day^{-1}. The source of variation in sap flow between those trees and the rest of the sample trees was unclear, but their contribution increased the overall mean J_s for *E.* regnans stands from 2.34 to 3.08 m^3 m^{-2} day^{-1}. .

4.3 Implications for long-term catchment water yields

Increasing frequency of wildfire due to climate change (Flannigan et al., 2009) can lead to a significant shift in species composition with long term consequences for catchment ET and water yield. Bowman *et al*. (2014) reported the potential collapse of *Eucalyptus delegatensis* population in the Australian Alps due to a quick succession of wildfires since 2002. Recurrent high-frequency wildfire may irreversibly shift the species composition of *E. regnans* forests to those dominated by *Acacia* spp. and/or other eucalypt species that recover through epicormic resprouting (Fairman et al., 2016; Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011). Unexpectedly low post-fire regeneration of *E. regnans* observed in some catchments after the wildfires in 2009 (Benyon & Lane, 2013) may result in an increase of *Acacia* stands or mixed stands in these catchments. Inventory of the mixed stands of *E. regnans* and *A. dealbata* at Road 8 indicated that both species could reach similar sapwood area per hectare (Table 2). Based on our observations, the conversion of large areas of catchment from *E. regnans* to *Acacia* may increase catchment water yield for several decades. The magnitude of the increase, however, may depend on the sapwood area of the replacing *Acacia* stands and E_t responses from understorey (shrub and fern) layer under *Acacia* overstorey stands. As some *Acacia* species are relatively short-lived, the longer-term consequences will depend on the type of vegetation that may eventually replace these *Acacia* stands in the absence of or as the result of further fires.

5 Conclusion

Strip-thinning altered the overstorey composition from *E. regnans* stands to *E. regnans* and *Acacia* stands, while a mixed *E. regnans - Acacia* stand was present 20 years after clear-felling iof *E. regnans*. Sap flow measurements showed that J_s and E_t of overstorey *Acacia* stands were lower than that of the overstorey *E. regnans* stands, while the g_c estimates indicated species-level physiological differences. Variation of $\mathrm{g_c}$ in response to maximum VPD at Road 8 suggests that stomatal regulation of *Acacia* may be more sensitive to VPD than *E. regnans*. Greater canopy interception of *Acacia* stands would offset about 13% of the difference in transpiration between species. Thus, replacement of *E. regnans* stands with *Acacia* stands may result in a reduction of catchment ET. However, the amount and persistence of this change will be influenced by total basal area of the replacement *Acacia* stands, E_t responses from understorey shrub/fern and frequency of wildfire that determine future succession dynamics.

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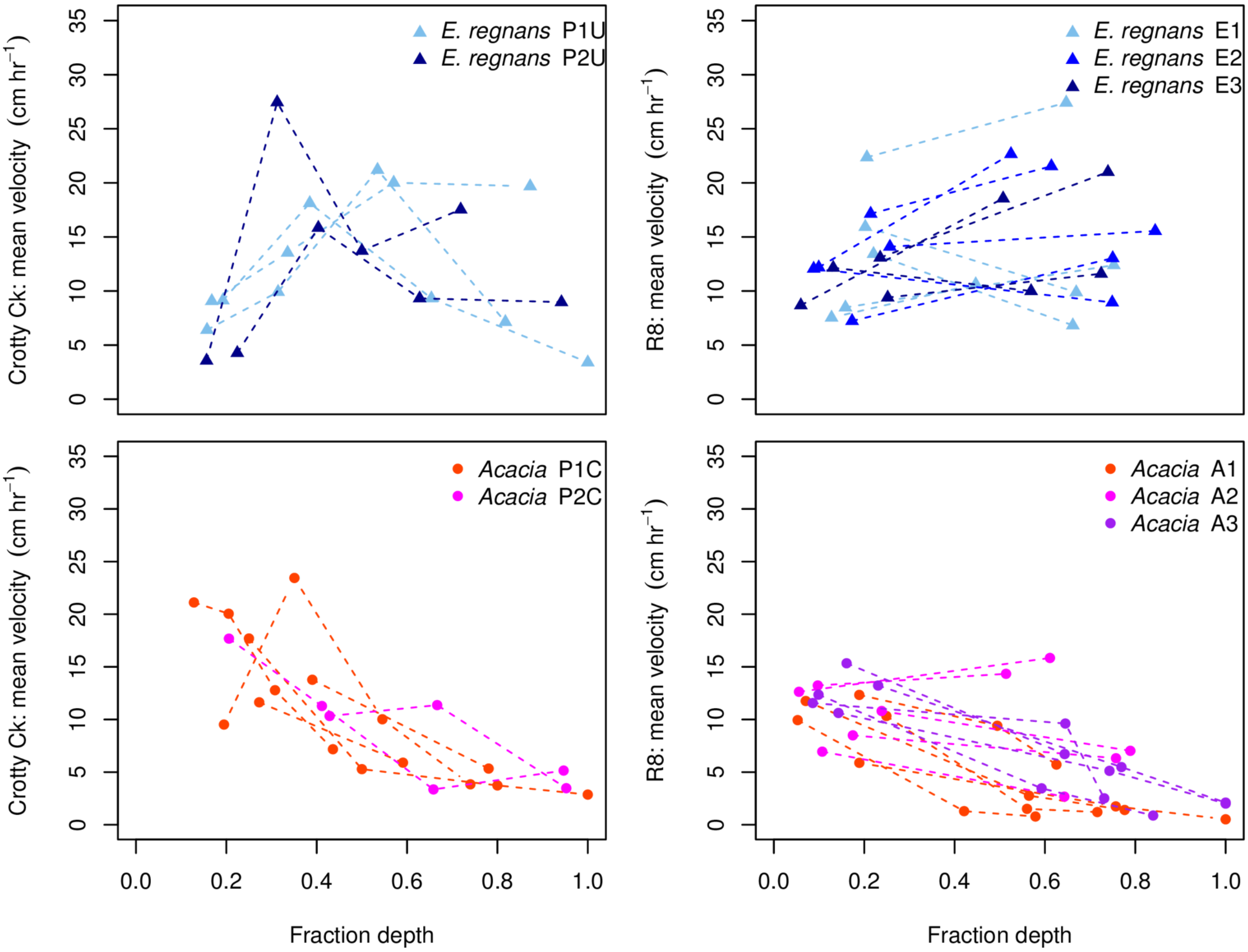

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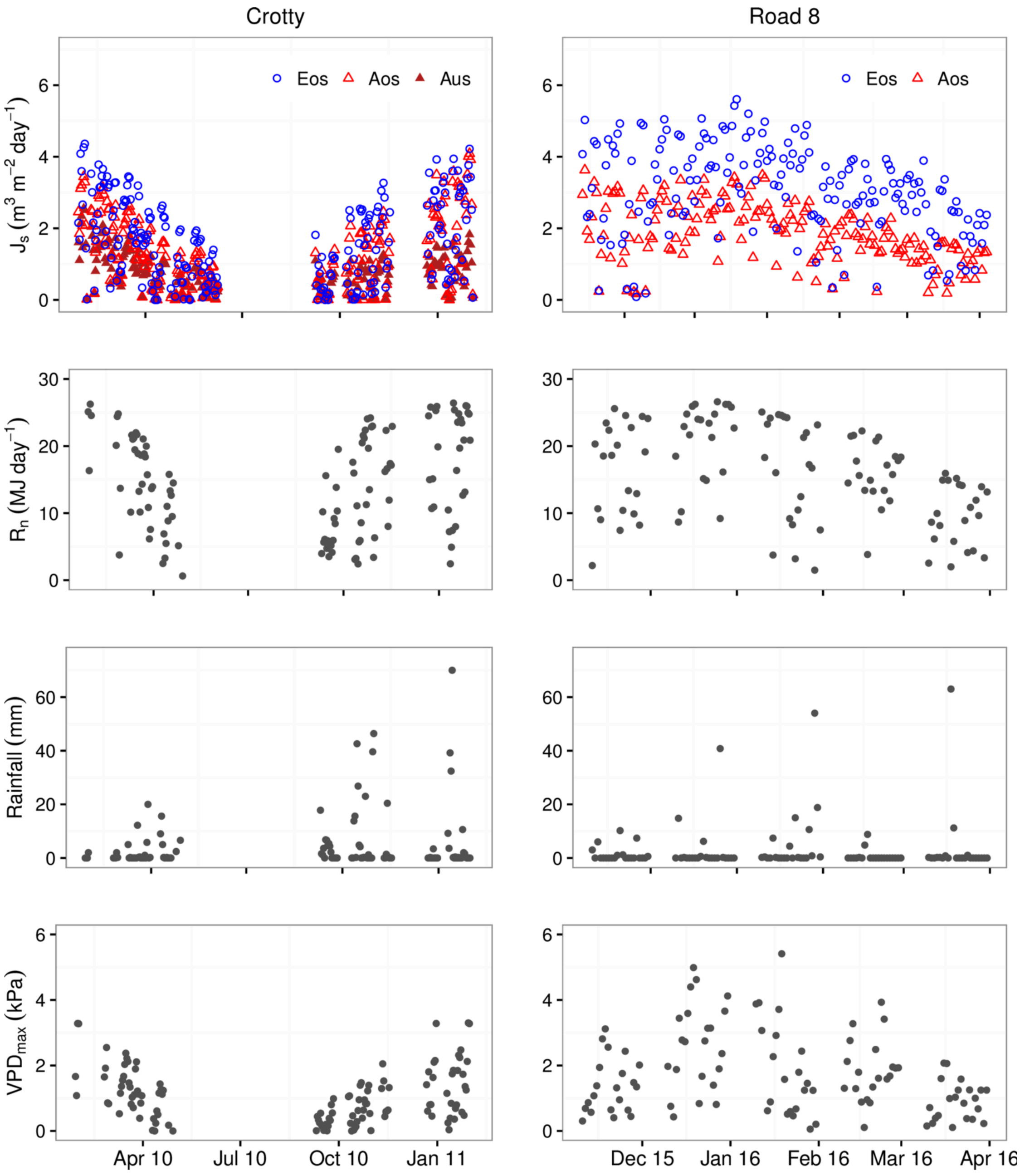

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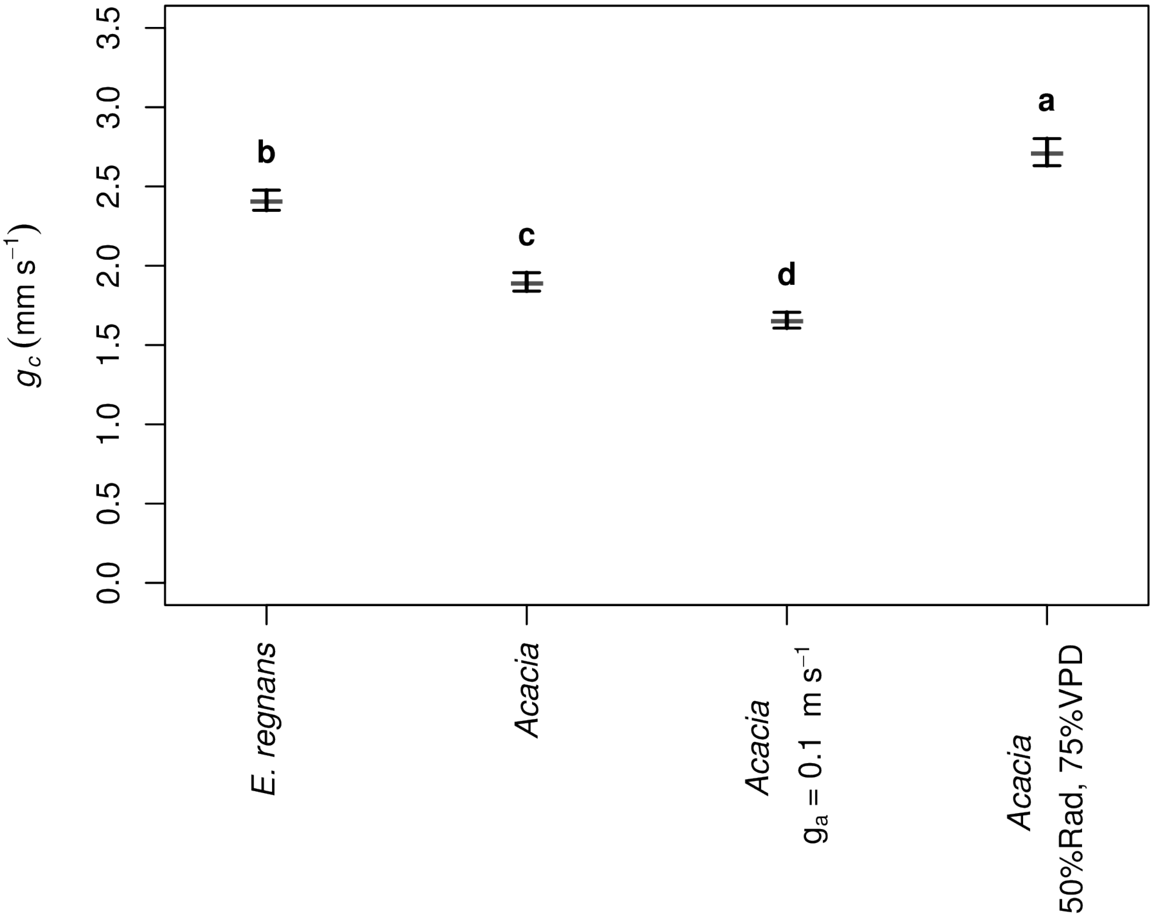

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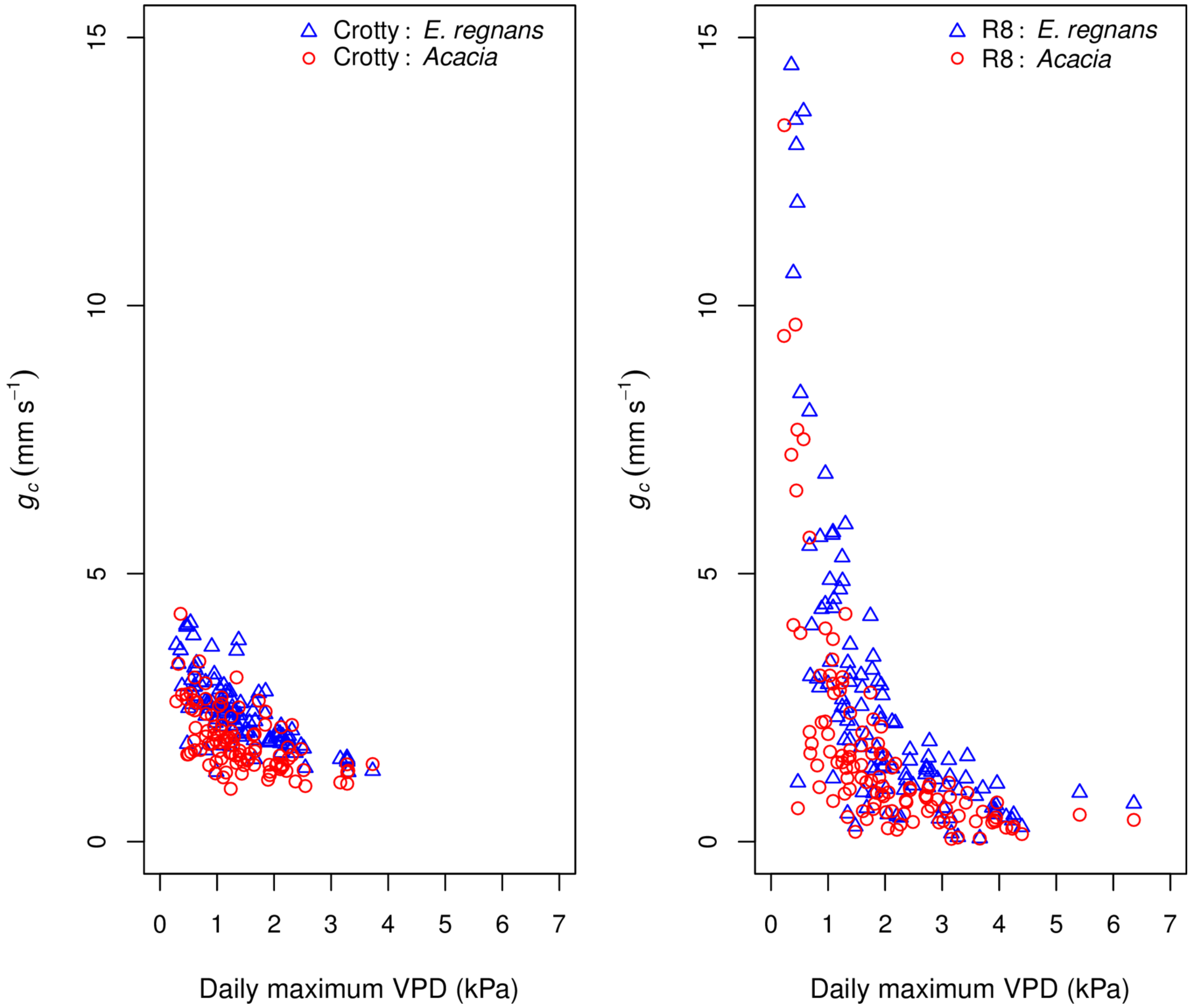

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1 List of Tables

Table 1. Topography and characteristics of sample plots in uncut and cut strips at Crotty Creek.

	P1U	**P1C**	**P2U**	**P2C**
Plot area (m^2)	225	225	300	225
Elevation (m AHD)	832.3	836.0	809.5	807.8
Slope (^{0})	14	11	15	15
Aspect (^{0})	9	3	344	358
Strip orientation	east - west	east - west	northeast - southwest	northeast - southwest
Overstorey species	*E. regnans*	*A. dealbata*, *A. melanoxylon*	*E. regnans*	*A. dealbata*, *E. regnans*[1]
Understorey species[2]	*.O argophylla*, *Z. arborescens*	*H. angustifolia*	*A. dealbata*, *P. aspera*, *C. lawrenciana*	*C. lawrenciana*
Overstorey basal area (m^2 ha^{-1})	88.2	23.3	56.1	26.9[1]
Understorey basal area (m^2 ha^{-1})[3]	-	-	2.3	-
Overstorey sapwood area (m^2 ha^{-1})	12.3	8.2	7.1	7.5[1]
Understorey sapwood area (m^2	-	-	0.9	-

ha^{-1})[3]

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[1] A post-thinning regrowth *E. regnans* tree was found in P2C (basal area of 0.04 m^2), but it has not been included in the overstorey basal area or sapwood area.

[2] The understorey layer also included smaller shrubs and ferns (e.g. *Prostanthera melissifolia*, *Dicksonia antarctica*).

[3] The understorey basal and sapwood areas were not measured except in P2U.

Table 2. Characteristics of the Road 8 sap flow sample (E1-E3 and A1-A3) and inventory (1-9) plots.

Plot	Plot area (m^2)	*Eucalyptus regnans*			*Acacia dealbata*		
		Density (stem and stem ha^{-1})	Mean dbh (cm)	SA (m^2 ha^{-1})	Density (stem and stem ha-1)	Mean dbh (cm)	SA (m^2 ha^{-1})
Sample plots							
E1	73	5 (684)	31.5	19.9	6 (820)	15.5	5.9
E2	101	7 (593)	28.6	14.0	3 (296)	16.3	2.2
E3	118	13 (1103)	26.3	18.9	3 (255)	13.3	1.3
A1	142	2 (141)	27.6	2.4	15 (1056)	19.9	12.2
A2	173	1 (58)	45.5	3.0	14 (811)	18.7	9.2
A3	77	0	-	0	9 (1169)	21.5	15.2
Inventory plots							
1	177	1 (57)	29.7	1.3	10 (1132)	20.2	13.7
2	177	2 (113)	30.6	3.4	11 (622)	22.0	9.1
3	177	5 (283)	34.8	9.3	13 (736)	17.1	6.4
4	177	18 (1019)	21.7	12.9	9 (736)	14.5	3.3
5	177	6 (340)	26.9	6.9	16 (905)	16.5	7.4
6	177	2 (113)	22.7	1.4	9 (509)	22.5	7.9
7	177	14 (792)	24.6	13.3	9 (509)	14.8	3.3
8	177	4 (226)	22.5	3.0	17 (962)	19.8	10.9
9	177	21 (1188)	20.6	14.0	16 (905)	10.1	2.8
Mean (n = 9)	177	459	26.0	7.3	780	17.5	7.2

Table 3. Characteristics of sample trees and the number of probes per tree at Crotty Creek.

Sites	Plot	Species	dbh (cm)	Sapwood area (cm^2)	Number of probes
Crotty	P1U	*E. regnans*	108.2, 70.0, 58.3	961, 641, 315	8, 4, 4
	P1C	*A. dealbata*	31.6, 20.2, 10.2, 17, 22.3	226, 109, 51, 91, 105	4, 4, 2, 2, 4
	P2U	*E. regnans*	78.9, 50.5	741, 326	4 per tree
		A. dealbata	17.6, 13.4	76, 43	4 per tree
	P2C	*A. dealbata*	25.8, 32.1	150, 219	4 per tree
Road 8	E1	*E. regnans*	37.4, 23.8, 33.9, 30.6, 27.4	449, 196, 312, 260, 240	2 per tree
	E2	*E. regnans*	26.6, 35.9, 34.6, 27.6, 24.2	183, 342, 324, 199, 145	2 per tree
	E3	*E. regnans*	29.5, 30.3, 31.4, 31.4 , 35	229, 247, 271, 273, 306	2 per tree
	A1	*A. dealbata*	22, 23.5, 23.7, 20.9, 24	110, 137, 210, 169, 179	2 per tree
	A2	*A. dealbata*	31.8, 22.1, 23.2, 30.4, 24.2	226, 157, 173, 290, 166	2 per tree
	A3	*A. dealbata*	17.8, 23.4, 24.9, 24.0, 25.2	83, 138, 131, 134, 160	2 per tree

Table 4. LiDAR system configuration and flight detail.

Sensor type	OptechALTM3100
Flight altitude (m)	800

Airspeed (km/hr)	220
Wavelength (Hz)	69
Pulse repetition rate (kHz)	100
Laser beam divergence (mrad)	0.3
Scan angle (degrees)	28
Mean footprint size (m)	0.16
Point density (point/m^2)	4

Table 5. Mean daily sap flux density (J_s) and stand transpiration (E_t) of *E. regnans* and *Acacia* spp, with standard error in brackets. Letters denote statistically significant difference ($p < 0.05$) between groups.

Variables	**Sites**	**Data period uses**	**Vegetation groups**			**Number of days**
			E. regnans overstorey	*Acacia* overstorey	*Acacia* understorey	
J_s (m^3 m^{-2} day^{-1})	Crotty	28 Jan 2010 - 31 Mar 2010, 22 Dec 2010 - 2 Feb 2011	2.33 (0.108) a	2.02 (0.098) b	1.12 (0.054) c	103
J_s (m^3 m^{-2} day^{-1})	Road 8	1 Dec 2015 - 31 Mar 2016	3.08 (0.11) a	1.80 (0.07) b	-	122
E_t (mm day^{-1})	Crotty	28 Jan 2010 - 31 Dec 2010	1.46 (0.005) a	0.95 (0.004) b	-	190
	Crotty	28 Jan 2010 - 31 Mar 2010, 22 Dec 2010 - 2 Feb 2011	2.15 (0.011) a	1.57 (0.009) b	-	94
E_t (mm day^{-1})	Road 8	14 Oct 2015 - 4 Apr 2016	2.67 (0.006) a	1.45 (0.004) b	-	174
	Road 8	1 Dec 2015 - 31 Mar 2016	2.68 (0.009) a	1.45 (0.005) b	-	122

Table 6. Estimated effective LAI of the overstorey vegetation in the sample plots.

Sites	Plots	Overstorey Species	LAI	Average LAI
Crotty	P1U	*E. regnans*	2.00	1.77
	P2U	*E. regnans*	1.53	
	P1C	*Acacia* spp.	1.42	1.55
	P2C[1]	*Acacia* spp.	1.68	
Road 8	E1	*E. regnans*	2.36	2.83
	E2	*E. regnans*	2.72	
	E3	*E. regnans*	3.41	
	A1	*A.dealbata*	2.83	2.55
	A2	*A.dealbata*	2.26	
	A3	*A.dealbata*	2.57	

[1] Excluding the estimated effective LAI of the post-thinning regrowth *E. regnans* in the plot.