May 07

Co-ordination of leaf area, sapwood area and canopy conductance leads to species convergence of tree water use in a remnant evergreen woodland

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Keywords: Canopy conductance, transpiration rate, sapflow, Huber value, tree size, tree water use.

Abstract

This paper compares rates of tree water use, Huber value, canopy conductance and canopy decoupling of two disparate, co-occurring tree species, in a stand of remnant native vegetation in temperate Australia in order to compare their relative behaviour seasonally and during and after a drought. The study site was an open woodland dominated by *Eucalyptus crebra* (a broadleaf) and *Callitris glaucophylla* (a needle leaved tree). Tree water use was measured with sapflow sensors and leaf area and sapwood area measured destructively on felled trees. Huber value was calculated as the ratio of sapwood area to leaf area. Diameter at breast height (DBH) of the stem was used as a measure of tree size. Canopy conductance was calculated using an inversion of the Penman-Monteith equation while omega (canopy decoupling) was calculated as described by Lu *et al.* 2003.

The relationship between DBH and daily total water use varied over the four measurement periods, with largest rates of water use observed in summer 2003/4, following a large rainfall event and the smallest maximum water use observed in winter 2003 when monthly rainfall was much less than the long-term mean for those months. Despite differences in the relationship between sapwood area and DBH for the two species, the relationship between daily total water use and DBH did not differ between species at any time. The same rates of water use for the two species across sampling periods arose through different mechanisms: the eucalypt underwent significant changes in leaf area whilst the *Callitris* displayed large changes in canopy conductance, such that tree water use remained the same for both species over the two year period.

Canopy conductance and the decoupling coefficient were both significantly larger in winter than summer in both years. The generally low decoupling coefficient (0.05 to 0.34) reflects the low leaf area index of the site. When evaporative demand was small (winter) the degree of stomatal control was small and the decoupling coefficient was large. There was no relationship between tree size and either canopy conductance or the decoupling coefficient. Transpiration rates generally showed little variation between seasons and between species because of the balance between changes in leaf area, canopy conductance and evaporative demand. The occurrence of a significant drought did not appear to prevent these co-ordinated changes from occurring with the result that convergence in water use was observed for these two disparate species.

Introduction

Obtaining estimates of rates of tree water use are important in investigations of ecosystem function and of catchment hydrology (Magnani *et al.* 1998, Pausch *et al.* 2000). Whilst it is axiomatic that variation in environmental conditions (especially solar radiation, atmospheric vapour pressure and soil moisture) influence tree and stand water use (Arneth *et al*. 1996, Zeppel *et al.* 2004), the relative behaviour of co-occurring contrasting life-forms (for example needle-leaved *versus* broadleaved species) is poorly known. Similarly, contrasting the impact of drought on co-occurring species that differ in habit has rarely been examined in the field, whilst the influence of tree size in determining tree water use and related behaviour is also unclear for Australian ecosystems. It is important to quantify the influence of habit and tree size on tree water use, leaf and sapwood area and other parameters because these factors have significant impacts on forest hydrology (Vertessy *et al*. 1998; Watson *et al*. 1999). Furthermore, different habits and trees of different sizes have different hydraulic architectures (Eamus and Prior 2001, McDowell *et al.* 2002) and such differences may influence additional functional features, including changes in stomatal and canopy conductance, rate of photosynthesis, transpiration rate and growth (Becker *et al*. 2000; Yoder *et al.* 1994; Brodribb and Field 2000; Hubbard *et al*. 2001; Macinnis-Ng *et al*. 2004). In a recent review Ryan *et al*. (2006) note that there remain significant inconsistency in the response of canopy conductance and transpiration rate to increased tree height, both within and across species.

Tree water use is influenced by leaf area and sapwood area (O'Grady, 2000; Martin *et al*. 2001), both of which are proportional to tree size (Kolb and Stone, 2000; Meinzer *et al*. 2001). Consequently an understanding of relationships among tree size, leaf area, sapwood area and water use are essential for predicting hydrological processes within forests (Vertessy *et al*. 1995). However, patterns of variation in these relationships between seasons, between drought and non-drought periods and between co-occurring species remain relatively poorly documented (Meinzer *et al*. 2001). As tree height increases, canopy leaf area per tree generally increases. However, total daily water use may increase with tree size (Martin *et al*. 1997; Andrade *et al.* 1998) or show no consistent trend (Wullschleger *et al*. 2000, Hatton and Vertessey 1990). This paper investigates the influence of tree size on tree water use for two co-dominant species differing in leaf form (broadleaf compared to needle leaved) across 2 years of study, during which time the stand of trees was subject to both drought and post-drought conditions.

The influence of hydraulic architecture on water transport through the soil-plant-atmosphere continuum is the subject of extensive research (Ryan *et al.* 2000; Meinzer 2001; Becker *et al*. 2000; Mencuccini 2002; McDowell *et al*. 2002 ; Mencuccini, 2003 ; Mokany *et al*. 2003; Zimmerman *et al*. 2004). Trees adjust their hydraulic architecture in relation to growing conditions, such as atmospheric and soil water content (Chaves *et al*. 2003; Mencuccini and Grace, 1994; Sellin, 2001; Whitehead and Beadle, 2004). Pipe theory (Mokany *et al*. 2003) predicts that for a given species, the ratio of sapwood area to leaf area should remain similar throughout the development of the plant (Waring *et al*. 1982). Whilst support for this prediction exists (Whitehead *et al*. 1984; Morataya *et al*. 1999) contradictory evidence has also been observed (Hubbard *et al.* 1999, Magnani *et al.* 2000). In the present study we examine the relationship between tree height and Huber value (Hv; ratio of sapwood area to leaf area) in remnant vegetation in temperate Australia across two seasons.

Whilst the influence of tree size (DBH or height) on tree water use has been investigated in many species, there appears to be little information about the influence of tree size on transpiration rate (rate of water transpired per unit leaf area per unit time). Although *a priori* reasoning may suggest no influence of tree size on transpiration rate (because leaf area is a component of both tree size and transpiration rate), the social status (emergent, co-dominant, suppressed) of the canopy of a single tree within the canopy depends on its height and a tree's social status influences the daily total rate of water use (Arneth *et al.* 1996, Martin *et al*. 1997). Furthermore, variation in canopy conductance and the degree of decoupling of a canopy (McNaughton and Jarvis 1983) vary with tree size (Martin *et al*. 1997, 2001) and these factors may contribute to variation in transpiration rate, as a function of tree size. In the present study we examine how canopy conductance, decoupling and transpiration rate vary with tree size.

The aims of the work described in this paper are to (a) compare the rates of water use of two disparate co-occurring tree species; (b) determine seasonal changes in relationships among tree size, leaf area, sapwood area, Huber value, omega and tree water use for these two species; (c) examine whether canopy conductance and omega vary with tree size and season; and (d) examine the influence of drought on these patterns and relationships.

Materials and Methods

Site description

The study site was located in remnant woodland on the Liverpool Plains, (about 90 km south of Tamworth) on the northwest plains of New South Wales, Australia (31.5° S, 150.7° E, elevation 390 m). Vegetation at the site consisted of open woodland, with an average height of 14 m, dominated by *Eucalyptus crebra* F. Muell. and *Callitris glaucophylla* J. Thompson and L.A.S. Johnson. These two species account for approximately 75% of the tree basal area at the site. Soils at the site were well drained acidic lithic bleached earthy sands (Banks, 1998) with pockets of clay. Total tree basal area for the site was 23.8 ± 3.4 m^2 ha^{-1} and leaf area index was generally about 1.0 to 1.2 throughout the year.

Weather, soil moisture content and leaf water potentials

Wind speed was measured with a cup anemometer located above the canopy, approximately 18 m above ground. Wind speed was measured every 15 s and hourly averages recorded on a Star Logger (Measurement Engineering Australia, Adelaide).

Rainfall data and aspirated wet and dry bulb temperatures were obtained from a screened climate station (Environdata Pty Ltd, Australia) located approximately 500 m from the study site in a cleared field (approximately 4 ha). Total solar radiation was measured above the screen. Vapour pressure deficit (VPD) was calculated from wet and dry bulb temperatures.

Volumetric soil moisture content was measured with an array of frequency domain reflectometry sensors which measure soil moisture by measuring the dielectric constant of soil (Theta Probe, ML2-X, Delta-T Devices, UK) in three plots. Theta probes were buried horizontally at 10, 40 and 50 cm in two plots, and at 10 and 40 cm in a third plot. Total soil moisture storage was calculated by multiplying the soil depth by the percent of moisture contained by the soil and then the water contained in each layer was summed. Relative water content was estimated by dividing actual daily soil moisture content by maximum soil moisture content over the entire season.

Water potential of three replicate leaves of three replicate trees of both species were measured in summer 2002/3, winter 2003, summer 2003/4, on between 1 and 3 days using a Scholander-type pressure bomb (Plant Water Status Console, Soil Moisture Equipment Corporation, USA). Fully expanded, sunlit, mature leaves were sampled in the outer canopy between 2 – 8 m height (using a hydraulic platform for access) between pre-dawn and 1700 h.

Leaf area, sapwood area, DBH, height and Huber values

Seven *C. glaucophylla* and eight *E. crebra* trees were destructively sampled in December 2002 (summer), June 2003 (winter), and January (summer) 2003. The DBH of each tree and the diameter of each branch (measured at the junction with the stem) were measured. Three branches from each tree were selected from the lower, mid- and upper-third of the canopy and the total projected leaf area of each branch determined using a leaf area meter (WinDIAS Delta-T devices Ltd, UK). *C. glaucophylla* leaves were examined under a binocular microscope, and were found to be a three sided. The projected area of photosynthetically active material only was measured on *C. glaucophylla.* A regression of branch diameter and leaf area for each species was then used to calculate the total leaf area per tree from the branch diameters of all branches for each individual tree. Regressions of DBH *versus* total branch diameter and individual branch diameter *versus* leaf area per stem were also calculated. This allowed an estimate of leaf area to be calculated from DBH using allometric relationships (Burrows *et al*. 2000; Santiago *et al*. 2000; Vann *et al*. 1998).

Sapwood cross-sectional area was measured on two, 5 mm diameter, cores, taken from the trunk at about 1.3 m height. Sapwood area was measured on each tree that was instrumented with Greenspan sap flow loggers. In addition, sapwood area was measured on trees that were felled. A distinct colour change was observed between bark, sapwood and heartwood in both species.

Diameter at breast height (DBH; ~1.3 m above the ground) was measured using a diameter tape and tree height was recorded after cutting the tree down. Huber value (Hv) was calculated by dividing by sapwood area (m^2) by leaf area (m^2).

Sap flow measurement

Sap velocity was measured using the heat pulse technique with commercial sap flow sensors (Greenspan Technology Pty Ltd., Warwick, Australia). Two probe sets (4 sensors) were inserted at 90 ° to each other in each tree. A preliminary Monte Carlo simulation showed that four probes per tree were adequate (Zeppel *et al.* 2004). A minimum of seven and a maximum of 15 trees were instrumented for each species at each sampling time.

Sap velocities were monitored at 15-minute intervals over a two-week period during July-August 2002 (mid-drought; winter), January-February 2003 (mid-drought; summer) July-August 2003 (post-drought; winter) and February-March 2004 (post-drought; summer). Tree water use was calculated for each sensor for twelve consecutive days after allowing two days for development of the wound that develops as a result of drilling into the wood (O'Grady, 2000; Olbrich, 1991). The weighted averages technique of Hatton and Wu (1995) was used to convert sap velocities to volume of transpired water.

Volume fractions of wood and water in the sapwood were determined gravimetrically on 5 mm cores taken from 10 trees of each species on two occasions. In *Eucalyptus crebra* the mean (and s.e.) wood fraction was 0.55 ± 0.03 and 0.50 ± 0.04 in winter and summer respectively. The mean water fraction was 0.23 ± 0.02 and 0.28 ± 0.01 in winter and summer respectively. In *Callitris glaucophylla* the mean wood fraction was 0.34 ± .01 in winter and 0.34 ± 0.04 in summer. The mean water fraction was 0.52 ± 0.01 in winter and 0.48 ± 0.03 in summer.

Radial sapflow profiles and wound width

Radial profiles of sap velocity through the sapwood of each species were determined to calculate the regions of maximum flow across the sapwood. Sap flow was measured at a minimum of 6 depths across the sapwood, replicated 3 or 4 times in different aspects in each tree. Knowledge of the region of maximum sap flow across the sapwood was used to calculate the depth to insert the sap flow sensors. The full method is described by O'Grady (2000).

The width of the wound around the holes used to insert the probes was measured twice in seven trees of each species, using a binocular microscope to measure the wound, using the technique described by O'Grady (2000). A wound width of 2.5 mm for *C. glaucophylla* and 3.7 mm for *Eucalyptus crebra* was used to correct velocity estimates.

Calculating canopy conductance and the decoupling coefficient

Maximum hourly canopy conductance (G_c) of each tree was estimated from hourly transpiration and climate data using the inverted Penman Monteith equation (Lu *et al.* 2003). Because there can be a time lag between transpiration at the canopy level, and sap flow in the tree stem 1.3 m above ground, due to stem storage of water in trees (Ewers and Oren, 2000; Lhomme *et al.* 2001; Schulze *et al.* 1985), it was necessary to estimate the length of this time lag so that transpiration rates and canopy conductances could be most accurately modelled with the Penman-Monteith equation (Martin *et al*. 2001, Phillips *et al*. 2002). Regressions between hourly values of transpiration (m^3 water m^2 leaf area h^{-1}) and radiation (MJ m^{-2}) on clear sunny days were performed for time differences of -1, 0, 1 and 2 h. The regression with the highest r^2 was determined to be the time lag, and regressions were performed for between two or three trees, for each sampling period (Winter 2002, $r^2 = 0.95$; Summer 2002/3, $r^2 = 0.72$; Winter 2003, $r^2 = 0.96$; and Summer 2003/4, $r^2 = 0.89$). Each season had a time lag of one hour, with the exception of Summer 2002/3, which had no time lag, possibly due to an extremely large rain event (93 mm) preceding the sampling period. Therefore a lag of one hour was used in all hourly time step calculations except Summer 2002/3.

Using transpiration as an input, canopy conductance ($G_{c,}$ mm hr^{-1}) was estimated using the equation:

$$G_c = [\lambda \Upsilon E_{hp}\ G_{a.}]/[\ (\Delta R_n) + (k\rho C_p D G_a)\text{-}\ (\lambda([\Delta + \Upsilon)\ E_{hp}] \qquad (1)$$

where λ is the latent heat of vaporisation (2.39 MJ kg^{-1}), Δ is the slope of the relationship between saturation vapour pressure and temperature (kPa $°C^{-1}$), R_n is net radiation intercepted by the forest canopy (MJ m^{-2} hr^{-1}) (54% of total radiation in this forest, M. Zeppel, unpublished data), ρ is air density (kg m^{-3}), C_p is the specific heat of air (1.013 MJ kg-1 ° C^{-1}), D is the vapour pressure deficit (kPa), G_a is aerodynamic conductance (m s^{-1}), Υ is the psychometric constant (0.066 kPa $°C^{-1}$), E_{hp} is transpiration measured using the heat pulse system, and k is a conversion factor, to convert values from seconds to hours.

A sensitivity analysis was conducted on the effect of variation in temperature on Υ and Δ on G_c. Varying temperature from 6 to 40 °C only changed G_c by 2%, therefore an ambient winter temperature of 13.5 °C in winter and 27.5 °C was assumed.

G_a is the inverse of r_a, aerodynamic resistance (s m^{-1}), which was estimated from the following equation (Yunusa *et al*. 2000):

$$r_a = 4.72(\ln (Z/Z_o))^2 / (1+ 0.54U) \qquad (2)$$

where Z is canopy height (m), Z_o is roughness height (1.95 m for this forest type, Hutley, pers comm), and U is wind speed (m s^{-1}). A conversion factor that was dependent on air temperature was used to convert G_c in mmol m^{-2} h^{-1} to mm h^{-1}.

The decoupling co-efficient (Ω) estimates the extent to which canopy transpiration is controlled by stomatal aperture in response to micrometeorological changes, and is dimensionless. Ω was calculated using (Lu *et al.* 2003):

$$\Omega = [\Delta/\Upsilon + 1] / [\Delta/\Upsilon + 1 + G_a/G_c] \qquad (3)$$

The decoupling coefficient ranges from zero to one. As Ω approaches zero, stomatal control of transpiration becomes stronger because the vapour pressure at the canopy surface becomes increasingly coupled to that in the bulk air (Lu *et al.* 2003).

Results

Weather and leaf water potential

Peak net radiation was about 4 MJ m^{-2} h^{-1} in summer and half of this in winter (Fig. 1a). Vapour pressure deficit was similarly larger in summer (2.1 kPa) than winter (1.1 kPa) and peaked later in the afternoon in summer than in winter (Fig. 1b). The long-term average annual rainfall for the Liverpool Plains is 680 mm, with approximately 50% of this occurring between October and February and 50% occurring from March to September (Fig. 2). However, rainfall between June 2002 and May 2003 was significantly less than the long-term average. Total rainfall in 2002 was 366 mm or 60 % of the 20-year average and total rainfall in 2003 was 522 mm 86% long-term average. In winter 2002, (June to August) rainfall was approximately 25 % of the average winter rainfall, while in summer 2002/3 (December to February) rainfall was approximately 60 % of the long-term average (Fig. 2). The period June 2003 to May 2004 received higher than average rainfall (Fig. 2).

Soil moisture

The relative water contents of the soil (RWC) at 10 and 40 cm depths are shown in Fig. 3. RWC of soil at 10 cm was more responsive to rain than soil at 40 cm. The RWC at 10 cm responded to rain events if the cumulative total over a 4 – 7 day period exceeded 10 – 15 mm. Thus, a number of small (> 10 mm) rain events on consecutive days influenced RWC, as well as large (> 20 mm) individual rain events. Single rain events of less than 10 mm had no effect at 10 cm or 40 cm. Soil at 40 cm responded to rain events larger than 20 mm and the response time was slower, and soil at 40 cm retained moisture for longer than soil at 10 cm.

Pre-dawn water potential for the eucalypt was very low (approximately -2.8 MPa) in summer 2002/3, reflecting the impact of the prolonged drought on plant water relations (Fig. 4a). Throughout the remainder of the day, eucalypt leaf water potential (ψ_w) declined to reach a minimum of -4.0 MPa (Fig. 4a). Pre-dawn water potential data are not available for *Callitris* because of equipment problems. However, in summer 2002/3, ψ_w of *Callitris* reached -5.0 MPa in late afternoon.

Pre-dawn leaf water potential of the eucalypt was higher (closer to zero) in winter 2003 than summer 2002/3. Similarly, ψ_w throughout the day were higher for both species in winter 2003 than summer 2002/3 (Fig. 4b). In the summer of 2003/4, after significant rains in the 3 months prior to the measurement of ψ_w, pre-dawn water potential for both species was higher than that observed in winter 2003 (Fig. 4c). However, the daily range of ψ_w in summer 2003/4 was similar to that observed in winter 2003, for both species. Generally, ψ_w of the *Callitris* was higher than that of the eucalypt, although this was not true for summer 2002/3. The difference in ψ_w was typically 0.5 to 1.0 MPa throughout the day, but the difference was generally smaller at the start or end of the day.

Sap velocity, tree size and tree water use

There was no significant relationship between tree size (DBH) and sap velocity for either species in either season (Zeppel, 2006). Sap velocity generally ranged between 10 and 45 cm h^{-1} for the eucalypt and 5 and 30 cm h^{-1} for *Callitris*. The relationship between tree size (DBH) and daily total water use varied over the four measurement periods (Fig. 5a-d). Maximum water use (*ca* 130 to 140 L d^{-1}) of large trees was measured in summer 2003/4, within 4 weeks of a significant (> 80 mm) rainfall event (Fig. 5d) and the smallest maximum water use (*ca* 30 L d^{-1}) for similarly sized trees was observed in winter 2003 (Fig. 5c) when monthly rainfall was much less than the long-term mean for those months.

The slope of the regression of leaf area and tree size was larger for the eucalypt than *Callitris* during summer 2003 and summer 2004 (Fig. 6). In winter this was not observed. For a mid - sized tree (DBH = 20 cm) the leaf area of the eucalypt was reduced by approximately 50% from summer 2003 to winter, while the leaf area of *Callitris* showed an approximately 25 % reduction. In winter, there was no difference in the slope of the regression of leaf area on DBH (Fig 6b).

As DBH increased, sapwood area increased significantly for both species (Fig. 7). For small trees (DBH <20 cm) the ratio of sapwood area: DBH did not differ between the 2 species, but for medium and large diameter trees, *Callitris* maintained a significantly larger sapwood area than the eucalypt (Fig. 7).

Huber value, canopy conductance, canopy decoupling coefficient and transpiration rate

Huber value was generally within the range 0.004 to 0.0012 for all measurement times and species (Fig. 8). There was no relationship between Huber value (Hv) and tree height for either species in either summer or winter (data not shown). Similarly, there were no differences in Hv between seasons or species (Fig. 8).

Canopy conductance ranged between approximately 80 and 380 mmol m^{-2} s^{-1} for the eucalypt (Fig. 9a). For the eucalypt, canopy conductance was significantly larger in winter than summer in both years, with the largest value obtained in the winter of 2002 and the smallest in the summer of 2003/4. In contrast, there was no consistent trend for *Callitris* with G_c being larger in winter than summer in 2003/2004 but smaller in winter than summer in 2002.

The decoupling coefficient was similarly significantly larger in winter than summer (Fig. 9b) for the eucalypt, with the largest value obtained in winter 2002 and smallest value in summer 2003/4 but there was no consistent trend for *Callitris.* The decoupling coefficient ranged in value between 0.05 and 0.34 across all sampling times.

Transpiration rate varied between 0.5 mm d^{-1} and 1.8 mm d^{-1} (0.5 and 1.8 L m^{-2} d^{-1}) for *C. glaucophylla* and 0.7 to 1.1 L mm d^{-1} (0.7 to 1.1 L m^{-2} d^{-1}) for the eucalypt (Fig. 9c). There was no significant difference in transpiration between seasons for the eucalypt but *C. glaucophylla* showed significantly larger transpiration rates in the summer compared to the winter. There was no relationship between tree size and transpiration rate for any season for either species (data not shown).

Discussion

Tree water use and transpiration rates

Sap velocity was independent of tree size for both species, a fact that makes scaling of individual tree water use to stand water use considerably easier than if sap velocity varied with tree size (Eamus *et al.* 2000; Meinzer *et al.* 2001). Independence of sap velocity from size has been observed previously (Oren *et al.* 1999, Vertessy *et al.* 2002) and this independence in velocity from size increases the confidence we can have in the scaled estimates of stand water use.

The severe and prolonged drought that affected Eastern Australia of 2002/3 was demonstrated in the period from July 2002 to June 2003, which received much less rainfall than the long-term average (Fig. 2). In contrast, the summer of 2003/4 received larger than average rainfall. The impact of this difference in rainfall between years is reflected in the leaf water potentials. Pre-dawn leaf water potential, an approximate indicator of soil water availability (Prior *et al*. 1997, Baldocchi *et al.* 2004), and mid-day values of leaf water potential were much lower in the summer (January and February) of 2002/3 than either winter (July to August) 2003 or summer 2003/4 (Fig. 4b-c). Similar relationships between leaf water potential and soil moisture have been observed in woodlands in Australian savanna (Prior *et al*. 1997), Mediterranean (Otieno *et al*. 2006) and tropical monsoon forest (Kume *et al*. 2007). Large differences in soil moisture and evaporative demand amongst measurement periods are likely to strongly influence leaf area, Huber value, canopy conductance and tree water use of this ecosystem and this is discussed later.

Rates of daily water use for large diameter trees were largest in the summer of 2003/4 (110 L d^{-1} for trees of 50 cm diameter) and smallest in winter 2003 (36 L d^{-1} for trees of 50 cm diameter) and winter 2002 (60 110 L d^{-1} for trees of 50 cm diameter). The rate of water use in summer 2002/3 was approximately 80 110 L d^{-1} for trees of 50 cm diameter. These patterns reflect both the impact of seasonality of radiation and vapour pressure deficit (Farrington *et al*. 1994, Stohr and Losch 2004, Wullschleger *et al*. 1998) and the influence of the drought. The winter of 2002 was 8 months into one of the worst droughts experienced in eastern Australia and this, coupled to reduced radiation and vapour pressure deficits in winter compared to summer explains the low rate of water use compared to either summer. The decrease in water use in winter 2003 compared to the winter of 2002 despite more rain in winter 2003 compared to winter 2002 is likely to be a result of a lag between the increased rainfall in winter 2003 and any increase in leaf area in response to that rain. Leaf flush is initiated in spring and consequently the potential for an increase in leaf area and hence water use was not observed until summer 2003/4, when leaf area per tree was much larger than that observed in winter 2003 (Fig 6).

Seasonal changes in leaf area are well documented for eucalypts and other tree genera (Williams *et al.* 1997; O'Grady *et al.* 1999) and result from seasonal changes in temperature and water availability (Myers *et al.* 1998). It is likely that eucalypts and some other genera may use changes in leaf area per tree to adjust rates of total daily tree water use (Eamus *et al.* 2000, Kume *et al*. 2007) during dry conditions. *Callitris,* in contrast to the eucalypt, showed smaller variation in leaf area than the eucalypt throughout the study period and, perhaps consequentially, exhibited a 25 % lower (more negative) minimum leaf water potential (-5.0 MPa) during the drought (summer 2002/3), than the eucalypt (– 4.0 MPa), supporting the conclusion that the eucalypt used changes in leaf area more effectively than *Callitris* to regulate tree water use and hence leaf water potential.

Within each measurement period the relationship between total daily water use (L d^{-1}) and DBH was the same for both species. Thus, for a given DBH, total daily water use was the same for both species. Such convergence of water use for sympatric species has been observed previously for broad leaved species (Calder *et al.* 1992; Enquist 2002; Hatton *et al.* 1998). However, this is the first example of such convergence for a broad leaf and a needle leaved species. Such convergence may arise because a species that routinely used less water than a competing adjacent species at a site would be at a competitive disadvantage because the competing species would have access to the unused water and would benefit (through nutrient uptake and the carbon gain associated with water loss from leaves) from use of that water. Meinzer *et al.* (2001) similarly observed that the relationship between sap flux density and tree size for 24 co-occurring species was the same for all species, indicating strong convergence in water use.

The rate of transpiration (rate of water transpired per unit leaf area per unit time) did not show any significant change between seasons for the eucalypt. Several coordinated changes may explain this lack of seasonal change in eucalypt transpiration rate. In the summer of 2003/4 after the drought had broken, water use per tree was largest, but leaf area per tree was also the largest (and consequently Huber value was smallest). Omega (Ω) was the smallest and therefore the coupling between the hot dry air of the summer at this site and the canopy was largest. To prevent too large a decline in leaf water potential (which were higher at this time than in previous measurement times) canopy conductance was lowest. This contrasts to winter 2003, when cooler daytime temperatures and smaller VPDs, coupled to the reduced leaf area per tree and hence much larger Huber values and a much larger Ω, resulted in a smaller demand for water supply to the canopy, a reduced level of water stress and consequently a much larger canopy conductance was maintained at this time. Finally, in summer of 2002/3, during the later part of the drought, low leaf water potentials were observed as a result of the low soil moisture content coupled with a large evaporative demand of the atmosphere, a small Ω and moderate leaf area and Huber value. These conditions resulted in a small canopy conductance being maintained. As a consequence of this coordination amongst changes in leaf area per tree, G_c, Ω and evaporative demand, transpiration varied much less between measurement periods than expected given the large difference in soil moisture, temperature and VPD that existed during drought and non-drought periods and winter and summer periods. A similar lack of variation in transpiration despite large variations in soil moisture, rainfall, VPD and leaf water potentials has been observed along a strong rainfall gradient in tropical Australia (Eamus *et al*. 2000). Similarly Hatton *et al*. (1998) concluded that transpiration rate of temperate eucalypts does not differ between species, whilst Meinzer *et al*. (1997) have also shown that transpiration rate for 4 co-occurring species in a tropical forest did not differ. These results support the view that transpiration rate is relatively conservative at a site (Magnani *et al.* 1998). More importantly, however, was strong convergence in rates of water use across the two species across all measurement periods across the full range of tree size. We suggest that this is because it is the rate of acquisition of water *per se* (with the associated uptake of nutrients and the carbon gain that is concomitant with water loss from the canopy) that determines competitive outcomes between co-occurring species rather than transpiration rate, which, as observed here, can differ between species without there being any difference in water use.

Transpiration rate of the *Callitris,* in contrast to the eucalypt, did vary between seasons and, also unlike the eucalypt, transpiration showed a larger response in the summer of 2003/4 after the drought had broken, compared to the drought period of summer 2002/3. *Callitris* showed no increase in leaf area between summer 2002/3 and summer of 2003/4, in contrast to the significant increase in leaf area observed in the eucalypt. Thus, water use was the same in the *Callitris* and eucalypt for all measurement periods through two different mechanisms. For the eucalypt, transpiration rate did not differ between summer 2002/3 and summer 2003/4 but leaf area increased and so total tree water use increased in summer 2003/4 compared to summer 2002/3. In contrast, transpiration rate increased in the *Callitris* but leaf area was relatively constant and so tree water use increased in parallel with the eucalypt between summer 2002/3 and summer 2003/4. The observed decline in G_c for *Callitris*, from 380 to 175 mmol m^{-2} s^{-1} for the period summer 2002/3 to summer 2003/4 is also in marked contrast to the lack of response of G_c for the same period for the eucalypt, further exemplifying the different mechanisms underlying the convergence of total tree water use observed for the two species.

Canopy conductance, omega and Huber values

Canopy conductance (G_c) in the present study ranged from approximately 80 to almost 400 mmol m^{-2} s^{-1} (Fig. 9a). This range agrees well with values determined for broad leaf oak forest, mixed coniferous forest, Amazonian rainforest and mature beech forest (Granier and Breda 1996, Harris *et al.* 2004, Martin *et al*. 1997, Magnani *et al.* 1998). There was no relationship between G_c and tree size for either species, as has been noted previously when G_c is expressed on a leaf area basis (Martin *et al*. 2001). Seasonal variation in canopy coupling (Ω) were significant and differed amongst species. Hutley *et al*. (2001) similarly observed seasonal changes in Ω, with large values in the wet season (where water vapour pressure deficits are small and soil moisture content large) and small values in the dry season (where the converse occurs). These seasonal changes indicate that when evaporative demand is small (winter in temperate Australia or wet season in monsoonal Australia) the degree of stomatal control of water loss is small, and Ω is consequently larger. Thus, canopy conductance (G_c) was larger in winter than summer in the present study and larger in wet seasons than in dry seasons.

Eamus *et al*. (2000) observed that along a strong rainfall gradient, the relationship between DBH and sapwood area was the same among different species within a single site, but different when comparing amongst species growing at different sites. Similarly, Meinzer *et al*. (2001) found a single relationship between DBH and sapwood area amongst 24 co-occurring tree species in Panama. The results of the present study do not support the convergence of a single relationship between DBH and sapwood area amongst the two species examined here. Similarly, the relationships between DBH and leaf area were different for the two species in summer. However, a single relationship between DBH and tree water use was observed for both species in the present site (as discussed previously). We suggest that the larger sapwood area per unit DBH observed for medium and large *Callitris* trees compared to the eucalypt, is a result of the smaller sapwood specific conductivity generally observed in conifers compared to broad leaved species (Tyree and Ewers 1996, Eamus and Prior 2001) and that differences in sapwood area, leaf area and leaf specific conductivity between the two species acted in concert to minimise differences in transpiration rate.

Values of Hv obtained in the present study (5 to 10 x 10^{-4}) compare well with the range obtained in a 4 ecosystem study in temperate Australia (2 to 16 x 10^{-4}; Macinnis-Ng *et al.* 2004). Macinnis-Ng *et al*. (2004) found a significant decrease in Hv in summer compared to winter, a result they attributed to the leaf flushing that occurred in the summer. In the present study the increase in leaf area observed after the drought was broken (summer 2003/4 was reflected in the small but not significant decrease in Huber values for both species. The lack of a strong response in the present study could be because of the influence of the prolonged (> 18 months) drought on leaf area and a resulting continued inhibition of the leaf expansion that would normally occur in the spring. Huber values can increase as trees become taller (McDowell *et al*. 2002, Schafer *et al*. 2000). As trees grow taller, Hv may increase to compensate for the increased path length that water must travel to reach the leaves (Hubbard *et al*. 1999). This increase in Hv with tree height is also predicted in a model developed by Magnani *et al*. (2000). In contrast, Mokany *et al*. (2003) and Fischer *et al.* (2002) showed a decreasing Hv with tree height in *Eucalyptus delegatensis* and *Pinus flexilis* respectively. Mokany *et al*. (2003) showed that sapwood specific conductivity (k_s) increased with tree height and concluded that this increase in k_s supports the view that increased tree height requires an increase in the ability of the stem to supply water to the canopy. In contrast to the majority of studies, no relationship between Hv and tree height was observed in either species in the present study. This could be because (a) the range of tree sizes was relatively small; (b) because of changes in sapwood specific conductivity with tree size (Phillips *et al*. 2002); or (c) drought during the preceding 18 months had masked any relationship between Hv and tree size because of the impact of drought on leaf area and stem growth (and hence sapwood area).

In conclusion, we note the following: seasonal variation in leaf area, canopy conductance, omega and tree water use was observed for the needle-leaved and broadleaved species in this remnant native woodland of temperate Australia. However, the relationship between tree size and total water use was the same for both species, suggesting significant convergence in the integrated hydraulic behaviour of the two species, despite significant differences in seasonal changes in leaf area between the two species and differences between species in the relationship between sapwood area and tree size for medium and large diameter trees. As a consequence of coordination of changes amongst Gc, leaf area, omega and evaporative demand, rates of transpiration did not show any significant change between seasons for the eucalypt but more importantly rates of tree water use did not differ between the two species at any time. The occurrence of a significant drought did not appear to prevent coordinated changes from occurring.

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