

Dry season conditions determine wet season water use in the wet–dry tropical savannas of northern Australia

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Summary Daily and seasonal patterns of transpiration were measured in evergreen eucalypt trees growing at a wet (Darwin), intermediate (Katherine) and dry site (Newcastle Waters) along a steep rainfall gradient in a north Australian savanna. Relationships between tree size and tree water use were also determined.

Diameter at breast height (DBH) was an excellent predictor of sapwood area in the five eucalypt species sampled along the rainfall gradient. A single relationship existed for all species at all sites. Mean daily water use was also correlated to DBH in both wet and dry seasons. There were no significant differences in the relationship between DBH and tree water use at Darwin or Katherine. Among the sites, tree water use was lowest at Newcastle Waters at all DBHs.

The relationship between DBH and tree leaf area was similar between species and locations, but the slope of the relationship was less at the end of the dry season than at the end of the wet season at all locations. There was a strong relationship between sapwood area and leaf area that was similar at all sites along the gradient. Transpiration rates were significantly lower in trees at the driest site than at the other sites, but there were no significant differences in transpiration rates between trees growing at Darwin and Katherine.

Transpiration rates did not vary significantly between seasons at any site. At all sites, there was only a 10% decline in water use per tree between the wet and dry seasons. A monthly aridity index (pan evaporation/rainfall) and predawn leaf water potential showed strong seasonal patterns. It is proposed that dry season conditions exert control on tree water use during the wet season, possibly through an effect on xylem structure.

Keywords: *Eucalyptus*, hydraulic architecture, rainfall gradient, sapwood area, stem diameter, transpiration.

Introduction

In the wet season of northern Australia, water availability is high and evaporative demand low. Tree water use is expected to be large to maximize carbon gain. As soil water availability declines and evaporative demand increases throughout the dry

season, tree water use should decline to prevent canopy desiccation. Such reasoning is supported by many studies undertaken at a range of scales and a number of locations. Leaf-scale measurements of stomatal conductance and tree-scale measurements of total leaf area show strong seasonal patterns (Eamus and Cole 1997, Prior et al. 1997a, 1997b, Williams et al. 1997) for many tree species in savannas of north Australia and elsewhere (Martin et al. 1994, Franco 1998). Similarly, tree water use, measured by sap-flow sensors (Farrington et al. 1994) and canopy-scale measures of transpiration based on eddy covariance, reveal seasonality of water use in Australia (Hutley et al. 2000) and Africa (Verhoef et al. 1996, Miranda et al. 1997). Finally, at a regional scale, Specht's analyses reveal seasonality in the relationship between the ratio (actual evapotranspiration)/(potential evaporation rate) and available water (Specht and Specht 1999).

In contrast to the studies cited above, O'Grady et al. (1999) observed that, for a savanna site around Darwin, tree water use is not seasonal. This finding was explained on the basis that rooting depth allowed access to sufficient water stored in the soil in the dry season to enable transpiration to proceed at rates little different from those observed in the wet season. Transpiration rates expressed per unit leaf area were significantly higher in the dry season than in the wet season because of increased evaporative demand. However, the Darwin savanna site is located at the wet end of the large (> 1200 mm) rainfall gradient over which savannas occur in northern Australia. It is not known whether such seasonality in tree water use occurs throughout this rainfall gradient.

Savannas of northern Australia cover about 25% of Australia, occurring across a steep rainfall gradient extending from Melville Island (≥ 2000 mm rainfall year⁻¹) to Newcastle Waters (about 500 mm year⁻¹) 1000 km inland to the south. We hypothesized that, as annual rainfall decreases and evaporative demand increases along this rainfall gradient between the northern and southern limits of savanna distribution, seasonality of tree water use (that is, the difference between wet and dry season water use) increases. We also examined how allometric relationships relating tree water use to three parameters of tree size (basal area, sapwood conducting area and tree leaf area) vary between location and seasons. Whitehead et al.

(1984) and Mencuccini and Grace (1995) proposed that functional relationships between leaf and sapwood area are influenced by site differences in soil water availability and evaporative demand. We investigated such relationships along the aridity gradient in savannas of northern Australia. Finally, we investigated the utility of relationships derived at one site for scaling tree water use at other drier sites in these savannas.

Materials and methods

Sites

Measurements were made at three sites along the North Australian Tropical Transect (NATT); Howard Springs (1700 mm year⁻¹; high rainfall), Katherine (900 mm year⁻¹; intermediate rainfall) and Newcastle Waters (500 mm year⁻¹; low rainfall). Soils at all sites were sandy loams. Howard Springs, approximately 35 km southeast of Darwin (130°45' E, 12°30' S), was dominated by *Eucalyptus miniata* A. Cunn. ex Schauer–*Eucalyptus tetradonta* F. Muell open forests. Mean tree height was approximately 15 m and basal area was 8–10 m² ha⁻¹. The understory is characterized by scattered small trees and shrubs with a seasonal grass component dominated by *Sorghum* spp. Rainfall is highly seasonal and occurs between November and April. Seasonal patterns of rainfall and pan evaporation for the nearest stations to each site are shown in Figure 1.

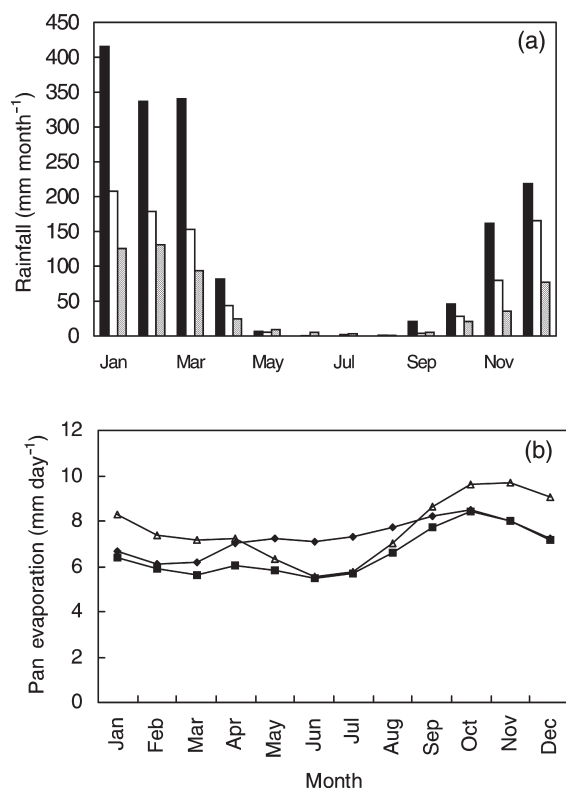


Figure 1. (a) Monthly rainfall at Howard Springs (filled), Katherine (open) and Newcastle Waters (gray), and (b) monthly pan evaporation at Darwin (◆), Katherine (■) and Newcastle Waters (▲).

Vegetation at the Katherine site (132°39' E, 14°40' S), approximately 360 km south of Darwin, was dominated by *E. latifolia* F. Muell–*E. tetradonta* open forests. Mean canopy height was approximately 12 m and basal area was approximately 7.5 m² ha⁻¹. Leaf area index of the canopy increased from 0.4 at the end of the dry season to 0.75 at the end of the wet season (A.P. O'Grady, unpublished data). *Sorghum* spp. dominated the understory, and understory shrubs were sparse.

Vegetation at the Newcastle Waters site (133°46' E, 17°07' S), approximately 750 km south of Darwin, was dominated by low open woodland of *E. terminalis* F. Muell and other *Eucalyptus* species. Mean canopy height was < 10 m and basal area was approximately 4.5 m² ha⁻¹. Leaf area index of the canopy was low, about 0.07, with little change between the wet and dry seasons (R.J. Williams, CSIRO, Darwin, unpublished data). The understory at the site was dominated by *Acacia* shrubs to a height of about 2 m.

Soil water availability

Predawn leaf water potential was used as a surrogate for soil water availability (Schulze and Hall 1982, Crombie et al. 1988). Leaf water potential was measured between 0630 and 0700 h on two randomly selected leaves on each of the trees instrumented with sap-flow loggers (see below). Measurements were made with a Scholander type pressure chamber (Soil Moisture Corp., Santa Barbara, CA). Data were analyzed as a fixed, two-factor analysis of variance with the factors season and location. Species was not included as a factor in the analysis, because it was not possible to have replicates of each species at each location. However, differences between species of similar phenological guilds within a site have been shown to be nonsignificant (Duff et al. 1997).

Monthly aridity index

We used a simple monthly aridity index calculated as the ratio of monthly mean daily pan evaporation rate to total monthly rainfall. When rainfall was zero in any month, we assigned a value of 0.1% of annual rainfall for that month, to avoid division by zero.

Sap-flow measurements

Tree water use was determined by the heat pulse technique with commercial sap-flow sensors (Greenspan Technology Pty. Ltd., Warwick, Australia). Estimates of heat pulse velocity were scaled to tree water use by the weighted averages technique of Hatton et al. (1990). Areas of conducting wood and bark thickness were determined from cores taken from the trees; sapwood was distinguished from heartwood by a distinct color change. The wood cores were used for determinations of volumetric wood and water fractions and a wound width of 3.1 mm was used to correct velocity estimates (O'Grady 2000).

Instruments were installed on five trees each of the two dominant eucalypt species at each location for 5 days at the end of the dry (August–September 1998) and wet (March–April 1999) seasons. Table 1 summarizes the species studied

Table 1. Trees sampled at three locations along the NATT.

Location	Species	DBH range (cm)	Leaf area range (m ²)
Howard Springs	<i>E. miniata</i>	8.8–30.4	7.4–111.8
	<i>E. tetradonta</i>	8.7–20.8	2.0–60.8
Katherine	<i>E. latifolia</i>	9.7–48.7	8.8–133.0
	<i>E. tetradonta</i>	4.9–48.7	2.0–95.7
Newcastle Waters	<i>E. spp.</i>	6.1–35.6	1.0–105.0
	<i>E. terminalis</i>	9.1–41.6	9.1–120.5

and the range of tree sizes sampled. Sap velocity was recorded at 15-min intervals and daily profiles were integrated to estimate daily tree water use. The diameter at 1.3 m height (DBH) and leaf area of each tree were recorded. Leaf area was estimated by the Adelaide technique (Andrew et al. 1979, O'Grady et al. 1999). The relationship between tree water use and diameter at breast height (DBH) was evaluated by analysis of covariance with factors season and location. Data were log–log transformed to restore linearity and reduce variance heterogeneity. Daily transpiration rates (Q_t , m³ day⁻¹ m⁻²) were analyzed as fully fixed two-factor analysis of variance with the factors season and location. Species was not included in the analysis because it was not possible to replicate for each species at each location. Species differences in transpiration rate within a site have previously been shown to be insignificant (Hatton et al. 1998).

Results

Aridity index and predawn water potential

Rainfall was seasonal at all three sites, with most (> 90%) rainfall occurring between November and April (Figure 1). The ratio of mean daily pan evaporation (PE), calculated for each month, to mean monthly rainfall (aridity index), was also seasonal, with peak values occurring in the dry season when daily evaporation rates exceeded rainfall. Figure 2 shows changes in monthly aridity index for the three sites. In the wet season, the aridity index was low and there were no differences among

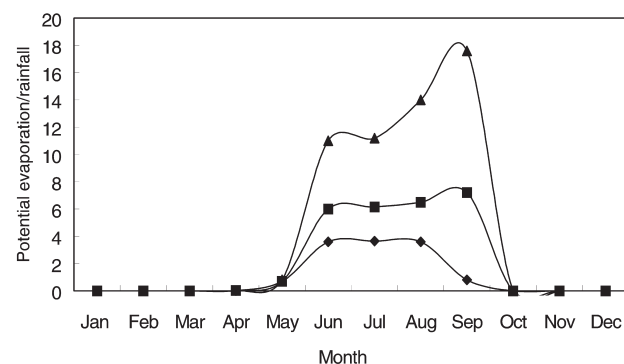


Figure 2. Changes in the monthly aridity index (monthly mean of daily pan evaporation rates/total monthly rainfall) for the three study sites (Darwin ◆; Katherine ■; Newcastle Waters ▲) along the North Australian Tropical Transect.

sites, reflecting the relative abundance of soil water compared with that in the dry season at a given site. However, as the dry season developed, the aridity index increased substantially. The aridity index was largest at Newcastle Waters and least at Darwin, with Katherine having an intermediate value.

Predawn leaf water potentials (Ψ_d) at each site during the wet and the dry season are shown in Figure 3. There were significant differences in Ψ_d between seasons and locations as well as a significant season \times location interaction (Season df = 1,106, $F = 870.2$, $P < 0.01$; Location df = 2,106, $F = 190.3$, $P < 0.01$; Season \times location df = 2,106, $F = 129.7$, $P < 0.01$). There were no differences in Ψ_d among sites at the end of the wet season and all values were higher than -0.4 MPa (close to zero), indicative of wet soils. However, Ψ_d was more negative at the end of the dry season than at the end of the wet season for all sites and the degree of difference between seasons increased with increasing latitude. Thus, Ψ_d was more negative at the end of the dry season at Newcastle Waters (-2.33 MPa) than at Katherine (-0.94 MPa) or Darwin (-0.49 MPa).

Relationships between DBH, sapwood area and leaf area

Sampling was conducted on five dominant eucalypt species at three locations along the NATT. Species sampled at each location and the range of tree sizes sampled for each species are given in Table 1.

Diameter at breast height (1.3 m) was an excellent predictor of sapwood area (SA; m²) in all species sampled along the NATT (Figure 4). Analysis of covariance showed that the slope of the relationship between sapwood area and DBH declined from Darwin, through Katherine, to Newcastle Waters (Figure 4) so that, at any given DBH, sapwood area was largest in trees at the Darwin site and smallest in trees at the Newcastle Waters site.

The relationship between DBH and tree leaf area was similar between species and locations, but the slope of the relationship was smaller at the end of the dry season than that at the end of the wet season (Figure 5). There was a strong relationship between sapwood area and leaf area that was similar at all sites along the NATT (Figure 6).

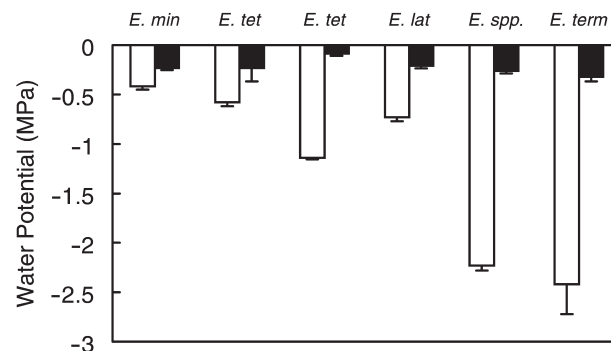


Figure 3. Predawn leaf water potential in the wet season (filled) and dry season (open) at Darwin, Katherine and Newcastle Waters. From left to right: *E. miniata*, *E. tetradonta* (Darwin), *E. tetradonta*, *E. latifolia* (Katherine), *E. spp.*, *E. terminalis* (Newcastle Waters).

Daily transpiration and tree water use

For all sites, daily transpiration rates (per unit leaf area; Q_l) were not significantly different between wet and dry seasons,

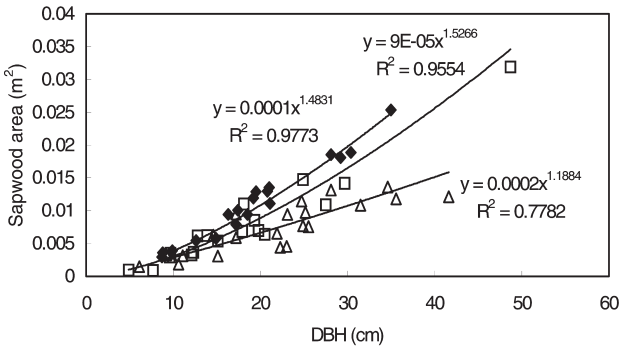


Figure 4. Relationship between DBH and sapwood area (SA) at three locations along the NATT: Darwin (◆), Katherine (□), Newcastle Waters (△). $SA = 8.0 \times 10^{-5} (DBH)^2 - 0.0004 (DBH) + 0.001$, $r^2 = 0.99$, $n = 30$.

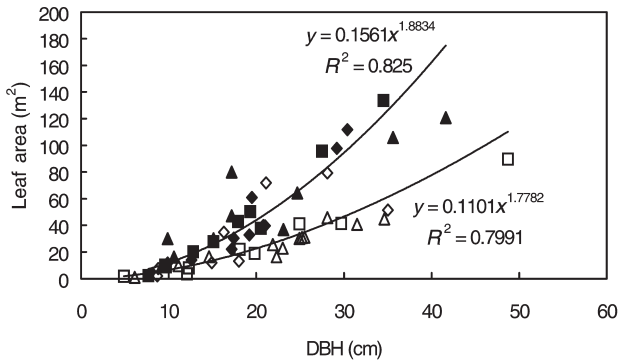


Figure 5. Relationship between DBH and leaf area in five eucalypt species at three locations along the NATT: Darwin (◆,◇), Katherine (■,□) and Newcastle Waters (▲,△). The slope of the relationship was less in the dry season (open symbols) than at the end of the wet season (filled symbols), $n = 30$ each season.

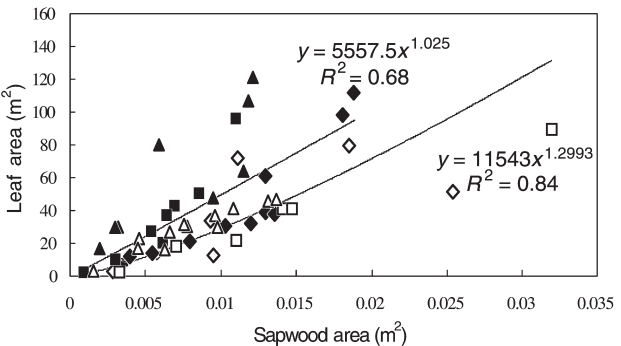


Figure 6. Relationship between sapwood area and leaf area for five eucalypt species at three locations along the NATT: Darwin (◆,◇), Katherine (■,□) and Newcastle Waters (▲,△). The slope of the relationship was less in the dry season (open symbols) than at the end of the wet season (filled symbols), $n = 30$ each season.

although transpiration rates were generally slightly higher in the dry season than in the wet season (Figure 7). Transpiration rates were significantly lower in trees at Newcastle Waters than in trees at either Katherine or Darwin, in both seasons. There were no significant differences in transpiration rates between trees growing at Darwin and Katherine in either season. Mean daily transpiration rates for each species at each location are given in Table 2. Mean Q_l was 0.00082 ± 0.0002 , 0.00064 ± 0.0002 and $0.00032 \pm 0.00008 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ at Darwin, Katherine and Newcastle Waters, respectively.

The diurnal pattern of transpiration for each location during the wet and dry seasons is shown in Figure 8. Transpiration increased during the morning and was at or near maximum rates by mid-morning and declined later in the afternoon, following a similar pattern to that of solar radiation. The early afternoon reductions in transpiration rates in Darwin (dry season) and Katherine (wet season) were associated with cloud buildup, which occurred on all measurement days at this time. Recovery of transpiration rates was evident later as cloud cleared. At Newcastle Waters during the dry season, transpiration rates declined steadily from a mid-morning maximum. This was not

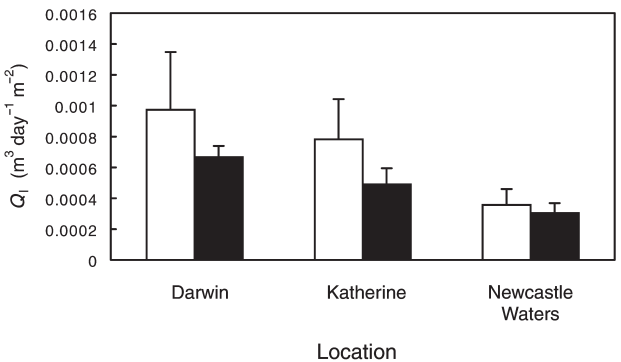


Figure 7. Mean daily transpiration rates during the dry (open) and wet (closed) season in trees at three locations along the NATT. Tree water use was significantly lower in trees at Newcastle Waters than in trees at either Darwin or Katherine.

Table 2. Mean daily transpiration rates for five eucalypt species at three locations along the NATT.

Season	Location	Species	$Q_l \text{ (m}^3 \text{ m}^{-2} \text{ day}^{-1}\text{)}$
Dry	Darwin	<i>E. miniata</i>	0.000464 ± 0.00018
		<i>E. tetrodonta</i>	0.0016 ± 0.0013
	Katherine	<i>E. tetrodonta</i>	0.00071 ± 0.00044
		<i>E. latifolia</i>	0.00084 ± 0.00032
	Newcastle Waters	<i>E. capricornia</i>	0.00035 ± 0.00016
Wet	Darwin	<i>E. terminalis</i>	0.00037 ± 0.00019
		<i>E. miniata</i>	0.00054 ± 0.00013
	Katherine	<i>E. tetrodonta</i>	0.0008 ± 0.00024
		<i>E. tetrodonta</i>	0.00021 ± 0.00013
	Newcastle Waters	<i>E. latifolia</i>	0.00071 ± 0.00022
		<i>E. capricornia</i>	0.00025 ± 0.00015
		<i>E. terminalis</i>	0.00036 ± 0.00025

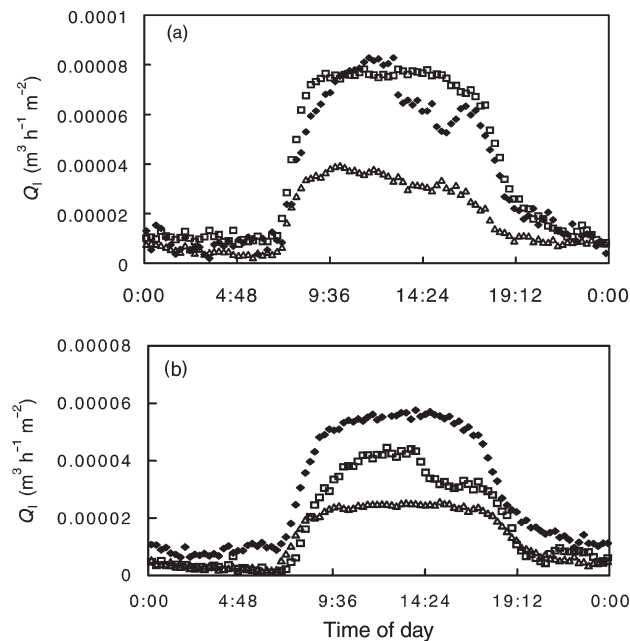


Figure 8. Diurnal patterns of transpiration in trees at Darwin (◆), Katherine (□) and Newcastle Waters (△) over a 5-day sampling period. Data represent the mean (a) dry season and (b) wet season transpiration rates for two species at each site.

a result of cloud cover because clouds were entirely absent at the time. During the wet season, transpiration rates were approximately constant between 0900 and 1630 h.

Mean daily water use was strongly correlated to DBH in both seasons at all sites (Figure 9) and water use was lower in the dry season than in the wet season ($F = 4.24$, $df = 1,52$, $P < 0.05$). However, the difference between the wet and dry seasons was small: 0.0161 and $0.0179 \text{ m}^3 \text{ day}^{-1}$ for dry and wet seasons, respectively. There were no significant differences in the relationship between DBH and tree water use at Darwin or

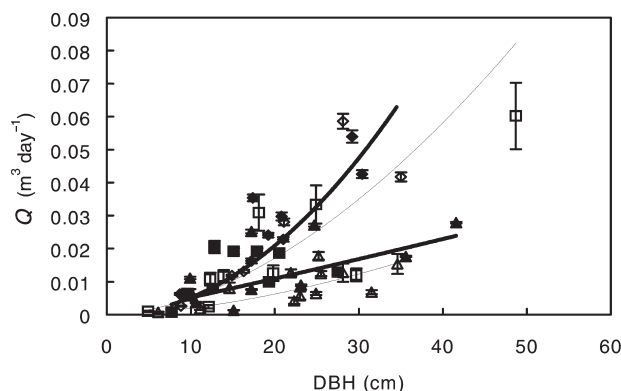


Figure 9. Mean daily water use in relation to DBH in trees at three locations along the NATT in the wet and dry seasons: Darwin (◆, ◇), Katherine (■, □) and Newcastle Waters (▲, △). Closed symbols and bold line represent the wet season and the open symbols and light line represent the dry season.

Katherine; however, tree water use was lowest at Newcastle Waters at all DBHs.

Discussion

Seasonal patterns of climate and tree water use along the NATT

Despite seasonality of rainfall, the aridity index and predawn water potentials, tree water use was aseasonal. The difference in water use between seasons for all sites was small, about 0.018 m^3 per day, or 10% of the daily rate (O'Grady et al. 1999), which showed large, interannual variation. In the present study, at Katherine, tree water use was slightly higher in the dry season compared with the wet season, but this probably reflects interannual variation (O'Grady et al. 1999). Trees at Newcastle Waters did not show a seasonal difference in water use in the present study. When the rains came at the start of the wet season, after a drought of up to 6 months, predawn water potentials increased significantly at all sites, but water use per tree did not increase significantly. We conclude, therefore, that tree water use does not vary significantly between seasons at any of the sites.

Because tree water use was measured at the end of the dry season, when the impact of declining soil water content was largest, tree water use averaged over the entire dry season will be larger than indicated by the present data, resulting in seasonal differences of less than the 10% average observed here.

The absence of a substantial increase in water use in the wet season compared with the dry season is contrary to previous findings based on leaf-scale (Martin et al. 1994, Pitman 1996, Eamus and Cole 1997, Franco 1998), tree-scale (Farrington et al. 1994, Dye 1996) and canopy-scale (Verhoef et al. 1996, Miranda et al. 1997) measurements. All of these studies showed significant declines in leaf and tree water use in the dry season.

Five possibilities exist to explain seasonal patterns in tree water use. First, tree water use in each season could be determined solely by the prevailing soil water availability. If this is true, water use should decline substantially in the dry season, compared with the wet season, for all sites. However, we observed that tree water use increased in the dry season at Katherine, from 0.135 m^3 per day to 0.181 m^3 per day per tree (data not shown). O'Grady et al. (1999) showed there was no significant difference in tree water use between seasons at Darwin. Together these data preclude the possibility that tree water use is controlled by soil water availability.

A second possibility is that low solar radiation and temperature limit water use to low values in both seasons, irrespective of water availability. However, at these tropical sites, both solar irradiances and daytime temperatures were high at all times and all sites.

A third possibility is that there is a continuous and abundant supply of soil water at all sites at all times of year. However, differences in Ψ_d between sites and between seasons indicated significant changes in soil water availability. Furthermore, the rainfall gradient between Newcastle Waters and Darwin is

large (about 1400 mm) and the aridity index so high in the dry season that we cannot conclude that soil water availability was non-limiting at all sites at all times during the year. The finding that water use per tree increased from Newcastle Water to Darwin as annual rainfall increased further supports the view that water availability was limiting.

A fourth possibility is that the rate of tree water use in both seasons is determined by the availability of water and rate of use in the wet season. By not over-expending water in the wet season, sufficient water is available at the start of the dry season to ensure an adequate supply throughout the dry season (Specht and Specht 1999). However, trees have no means of determining the duration and intensity of a forthcoming dry season in order to moderate current wet season water use. We also note that wet season rainfall at the Darwin site has varied between 1650 mm and 2400 mm over the past 5 years, and dry season duration and the timing of the start and end of the dry season is highly variable (Taylor and Tulloch 1985).

We propose that water availability in the dry season determines rates of water use in both the dry and wet season, resulting in aseasonal water use at all sites along the rainfall gradient.

Several studies suggest a hydraulic limit to water use. Leaf area/sapwood area ratio, sapwood area, leaf area and hydraulic conductivity are influenced by site differences in vapor pressure deficit (Mencuccini and Grace 1995, Whitehead 1998). The hydraulic architecture of trees is structured such that runaway embolisms are just prevented (Tyree and Sperry 1989, Tyree and Ewers 1996). Hydraulic conductance of stems of *Pinus ponderosa* Dougl. ex Laws can limit stomatal conductance, and stomatal responses to soil and atmospheric water content can be explained by hydraulic architecture (Bond and Kavanagh 1999, Hubbard et al. 1999).

In the dry season, evergreen trees transpire at rates equal to (Darwin), slightly higher than (Katherine) or lower than (Newcastle Water) the corresponding rates in the wet season. We suggest that the hydraulic architecture of these evergreen eucalypt trees is constructed to prevent runaway embolism under dry season conditions, and that, as site aridity increases, whole-tree hydraulic conductance decreases. Vulnerability to embolism is primarily determined by xylem and pit membrane pore diameter (Tyree and Ewers 1996). Wide xylem conduits and pit pores have a low resistance to water flow but exhibit high sensitivity to embolism. As annual rainfall declines along a rainfall gradient and the dry season progresses, soil water availability declines and therefore plant water potential must decline to continue to extract water. Xylem and pit-pore diameter must be small enough to prevent excessive embolism at the water potentials experienced during the dry season. Consequently, resistance to flow will be larger at drier sites and this sets an upper limit on the rate of water use per tree, assuming a sustainable water potential is maintained. Myers et al. (1997) noted that the difference between Ψ_d and midday water potential is the same in both wet and dry seasons. Thus, within a species, the gradient in water potential up a tree is constant, even at different sites (Mencuccini and Grace 1995), and water use

will remain constant if hydraulic conductance does not vary seasonally. Conversely, because water use does not vary seasonally, and the water potential gradient between root and leaf appears to be relatively fixed, hydraulic conductance of the conducting system must also be aseasonal. Finally, xylem structure, once formed, is relatively fixed and apart from the effects of embolisms, is unlikely to vary. Evidence that xylem structure does not change seasonally includes the finding that as xylem is crushed on the inner face through stem growth, new xylem with similar properties is formed. Also, seasonal changes in percentage embolism are very small in *E. tetradonta* (Prior and Eamus 2000), indicating that xylem tissues formed at different times of year behave similarly. Tognetti et al. (1997) have shown that whole-tree hydraulic conductance is lowest in trees derived from seed taken from the most arid sites, as predicted from the mechanism we propose and suggesting a genetic component to xylem characteristics.

Total water use per tree declined from Darwin through to Newcastle Water, because of the decline in annual rainfall along the NATT and the effect of a hydraulic architecture that has evolved to cope with an increasingly stressful dry season. Based on the assumptions that hydraulic architecture is determined by dry season conditions and this structure imposes a limit on wet season water use, we predicted that water use per tree would be lower at the drier sites, even in the wet season when water availability is high compared with the dry season. This prediction is supported by the data. Our data also support the view that hydraulic limits, resulting from differences in water availability (Ryan and Yoder 1997), limit tree height, with concomitant impacts on tree water use. Tree height declines along the rainfall gradient of north Australia (Williams et al. 1996).

The diurnal pattern of tree water use was similar at the three locations. During the wet season, changes in solar radiation input were reflected in changes in transpiration rate, whereas during the dry season, stomatal limitations to transpiration rates increased throughout the day, especially at Newcastle Waters.

Tree size relationships

Leaf area, sapwood area and DBH (or cross-sectional basal area) are commonly used to scale tree water use. We found strong relationships between DBH and sapwood area as noted by Vertessy et al. (1995) and Hatton et al. (1995). Our data suggest that sapwood area could be estimated for the major eucalypt communities of northern Australia from existing vegetation data sets that contain information on basal area and stem density (Wilson et al. 1990). This makes it an important and useful parameter for regional scaling of tree water use. Similarly, Dunn and Connor (1993) used sapwood area to scale water use in the *E. regnans* F. J. Muell forests of Victoria. They demonstrated a decline in sapwood area with forest age and correlated this to a decline in water use in these older forests. The use of scaling parameters such as basal area and sapwood area has been criticized, because of the seasonal relationship between tree water use and leaf area. However, in our

study, there were no seasonal differences in tree water use. Therefore, scaling tree water use based on parameters such as basal area is justified and may be preferable to leaf area because detailed estimates of spatial and temporal variation in leaf area are lacking.

Mencuccini and Grace (1995) reported that trees growing on sites differing in evaporative demand adjust their leaf area/sapwood area. Based on a combination of the Penman-Monteith equation and the Darcy equation to link evaporative demand and hydraulic architecture, it has been proposed (Whitehead and Jarvis 1981, Whitehead et al. 1984) that adjustments to sapwood and leaf areas occur in response to site differences in supply and demand for water. In our study, the leaf area to sapwood area ratio declined in the dry season at all sites and was the result of leaf loss. A decline in leaf area during the dry season is consistent with previous studies demonstrating a 30–40% decline in leaf area of evergreen eucalypts during the dry season (O'Grady et al. 1999). This decline is presumably a mechanism for controlling water use during the dry season. It is well known that stomatal conductance declines at high vapor pressure deficits (Eamus and Cole 1997, Prior et al. 1997a, 1997b). However, Saugier et al. (1997) noted that the decline in stomatal conductance alone was not enough to limit transpiration rates in boreal pine. We suggest that reducing leaf area rather than reducing stomatal conductance in the dry season represents an optimization response (Thomas et al. 1999a, 1999b) to increased evaporative demand. If leaves are not lost, conductance would be so low (to reduce transpiration rates sufficiently) that assimilation would be severely limited by CO₂ supply. However, as we have observed, the concentration of CO₂ in leaves in the dry season is not reduced to values that limit photosynthesis (Eamus and Cole 1997, Eamus et al. 1999).

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