

Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia

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Summary Australian savannas exhibit marked seasonality in precipitation, with more than 90% of the annual total falling between October and May. The dry season is characterized by declining soil water availability and high vapor pressure deficits (up to 2.5 kPa). We used heat pulse technology to measure whole-tree transpiration rates on a daily and seasonal basis for the two dominant eucalypts at a site near Darwin, Australia. Contrary to expectations, transpiration rates were higher during the dry season than during the wet season, largely because of increased evaporative demand and the exploitation of ground-water reserves by the trees. Transpiration rates exhibited a marked hysteresis in relation to vapor pressure deficit, which was more marked in the dry season than in the wet season. This result may be attributable to low soil hydraulic conductivity, or the use of stored stem water, or both. Tree water use was strongly correlated with leaf area and diameter at breast height and there were no differences in transpiration between the species studied. These results are discussed in relation to scaling tree water use to stand water use.

Keywords: Australian savannas, *Eucalyptus miniata*, *Eucalyptus tetradonta*, sapflow, vapor pressure deficit.

Introduction

Savannas occupy approximately 25% of the Australian continent and are restricted to tropical and subtropical zones where mean annual rainfall is greater than 500 mm. The composition and structure of savannas appear to be governed largely by soil water availability and, to a lesser extent, by plant available nutrients (Williams et al. 1996). Climate of the region is monsoonal. Mean annual rainfall is 1600 mm, of which 95% falls during the wet season (Taylor and Tulloch 1985, Duff et al. 1997), which is characterized by low vapor pressure deficits. The 5- to 7-month dry season is characterized by high vapor pressure deficits. Daily temperatures and solar insolation remain high throughout the year (Wilson et al. 1990).

Transpiration represents a major pathway for the discharge of soil and groundwater (Pidsley et al. 1994); however, this process is poorly understood in Australian savannas. Increasing demand for water by mining, pastoralism, urban development and tourism has created a need for a better understanding of the role of vegetation in the water balance of the region, to

manage water resources sustainably. Recent studies of leaf-scale processes of important savanna species (Duff et al. 1997, Myers et al. 1997, Prior et al. 1997a, 1997b, Williams et al. 1997) have shown that stomatal conductance and leaf water potential decline during the dry season in response to increasing vapor pressure deficits and declining soil water availability (Duff et al. 1997, Myers et al. 1997, Prior et al. 1997a, 1997b). Although leaf-scale studies are important contributors to the development of our understanding of the ecophysiology of plant communities, extrapolation of these studies to the scale of whole-tree or stand responses to the environment is difficult. We have used heat pulse technology (Dunn and Connor 1993, Farrington et al. 1994, Hatton et al. 1995, Vertessy et al. 1995) to examine spatial and temporal patterns of tree water use in the two dominant eucalypt species occurring in open forests near Darwin in northern Australia; *Eucalyptus miniata* A. Cunn. ex Schauer and *Eucalyptus tetradonta* F. Muell. These eucalypts contribute more than 80% of the leaf area index and biomass of these forests (Dunlop et al. 1995, O'Grady unpublished data); therefore, they may be assumed to have considerable influence on forest water balance.

We tested the hypothesis that daily patterns of transpiration (Q_t) vary among seasons and species and in relation to vapor pressure deficit. We also investigated whether it is possible to scale measures of whole-tree water use to estimate stand water use in the mixed open forests of northern Australia.

Methods

Site description

The study site was located in an *E. miniata*–*E. tetradonta* open forest (*sensu* Specht 1981) about 50 km south-east of Darwin (130°45' E, 12°30' S), Australia. The site was chosen because of its close proximity to a series of nested piezometers, neutron moisture meter access tubes and a weather station that logged temperature, relative humidity, light, wind speed, and wind direction. Vegetation at the site is characterized by an open canopy (less than 50% cover) of evergreen eucalypt trees with a mean canopy height of about 15 m. Leaf area index was typically low (about 1.0) and mean basal area was 8–10 m² ha⁻¹. The understory consisted of semi-deciduous and deciduous small trees and a seasonally continuous cover of annual

and, to a small extent, perennial grasses. Seasonal changes in overstory leaf area index were small; however, understory leaf area index changes dramatically over the wet season with *C₄ Sorghum spp.* dominating. These species senesce early in the dry season and thereafter understory leaf area index remains low (approximately 0.2) for the remainder of the dry season. Soils at the site are highly weathered sandy-clay laterites, and groundwater water levels vary between 1 and 15 m below the soil surface (Pidsley et al. 1994). Insolation, rainfall, temperature, humidity, wind speed and wind direction data have been recorded at the site since early 1994.

Mean hourly vapor pressure deficits (VPD) were larger in the dry season than in the wet season and peaked in the early afternoon in both seasons. Vapor pressure deficit varied from about 0.5 to 2.5 kPa in the dry season and from 0.1 to 1.5 kPa in the wet season. Mean hourly temperatures were higher in the wet season (ranging from 23 to 31 °C) than in the dry season, when temperatures varied from 18 to 30 °C (Figure 1). Rainfall totals for the area were 1536, 2174 and 1800 mm for 1994, 1995 and 1996, respectively. Mean monthly evaporation and rainfall calculated for Darwin airport for the three-year period are shown in Figure 1 (Bureau of Meteorology).

Soil water availability

Predawn leaf water potentials were recorded monthly during 1994 with a Scholander-type pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA). One leaf from each of five randomly selected individuals of five species: *E. miniata*, *E. tetradonta*, *E. porrecta* S.T. Blake, *Erythrophloeum chlorostachys* (F. Muell.) Baillon, and *Terminalia ferdinandiana* Exell, was sampled at each measurement period, although *T. ferdinandiana* is a dry-season deciduous species and was not sampled between May and October. The five species con-

tribute more than 95% of the standing biomass at the site (O'Grady unpublished observations). Leaf water potential measurements were used for surrogates of soil water availability (Schulze and Hall 1982).

Sapflow measurements

Tree water use was determined by heat pulse techniques with commercially available sapflow sensors (Greenspan Technology, Warwick, Australia). Heat pulse velocity measurements were scaled to tree water use measurements by the weighted averages technique of Hatton et al. (1990). The nomenclature used follows that recommended by Edwards et al. (1996). Conducting wood area was determined from wood cores, and sapwood was distinguished from heartwood by a distinct color change. The wood cores were used for determinations of volumetric wood and water fractions. Wounding was investigated by staining the sapwood area with diluted food dye after 5 days of instrumentation. A lateral wound with a mean width of 3.1 mm was used. The leaf area of each tree was estimated visually, based on the number of leaf modules on the tree (Andrew et al. 1979). The area of reference leaf modules was determined with a Delta-T leaf area meter (Delta-T Devices, Cambridge, U.K.).

Seasonal patterns of transpiration

Three *E. miniata* and three *E. tetradonta* trees were instrumented during the wet and dry seasons over a three-year period (1995–1997). Trees were randomly selected and different trees were used for each sampling block. Heat pulse velocities were recorded at 15-min intervals for up to two weeks during each season. Mean daily transpiration rates (Q_t) were analyzed as a fully fixed, three-factor analysis of variance with year, season and species as the factors.

Spatial patterns of transpiration

Spatial variations in transpiration rates were investigated at separate locations within the catchment area during the 1997 dry season. Each of the locations represented an extensive stand of *E. miniata*–*E. tetradonta* open forest. At each stand, two sites of approximately 1 ha were selected randomly within 500 m of each other. Three trees of both *E. miniata* and *E. tetradonta* were chosen at each site. Tree water use was measured on each tree for three complete days after instrumentation. Because of an insufficient number of sapflow loggers, not all trees could be instrumented at the same time. Instrumented trees were chosen randomly and the period of measurement within which all trees were instrumented was about six weeks. Measurements were conducted during July–August (dry season) and climatic conditions over the period were stable with little variation in day to day temperatures, solar radiation and vapor pressure deficits. Data were analyzed as a four-factor repeated measures analysis of variance.

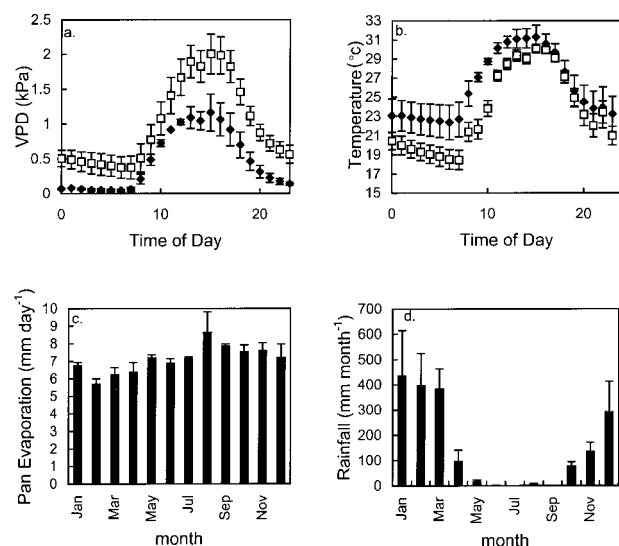


Figure 1. Diurnal variation in mean hourly (\pm SE) vapor pressure deficit (a) and temperature (b) during the wet (\blacklozenge) and dry (\square) seasons. Mean daily pan evaporation (\pm SE) at Darwin Airport (c) and mean monthly rainfall (\pm SE) at Howard Springs (d) for 1994–1996.

Results

Predawn leaf water potential responses

Predawn leaf water potential declined throughout the dry season from a high of -0.2 MPa to a low of -1.8 MPa in October and recovered rapidly with the onset of wet season rains (Figure 2). This pattern was similar to that reported by Duff et al. (1997) for a savanna site nearby, and reflects the decline in water available to roots over the dry season.

Species comparisons

Transpiration rates were similar for both species at all sampling times and across the catchment area. Tree water use was strongly correlated with diameter at breast height (DBH) and leaf area, and both species could be described by similar daily flux–scalar relationships. Diameter at breast height was consistently a better predictor of tree water use than leaf area ($r^2 > 0.75$), reflecting the greater accuracy with which DBH can be measured. The relationship was similar throughout the study period. An example of the relationship between daily flux and DBH during the dry season is shown (Figure 3). Mean daily transpiration rates for both species over the three-year sampling period are shown in Figure 4. If sampling had been limited to one year, for example 1994 or 1997, differences in the transpiration rates of the two eucalypts may have been inferred, whereas in reality the differences are mainly the result of tree-to-tree and year-to-year variability.

Daily transpiration

Diurnal patterns of transpiration (Q_1) were similar for both species and seasons. An example, *E. miniata* in the dry season 1995, is shown in Figure 5. Typically, Q_1 increased rapidly in the morning as VPD and radiation increased and generally reached a maximum by about midday, declining again during the afternoon. Transpiration rates exhibited hysteresis in relation to vapor pressure deficits. Thus, Q_1 was slightly larger for a given VPD during the morning than during the afternoon. This probably represents the effects of declining leaf water

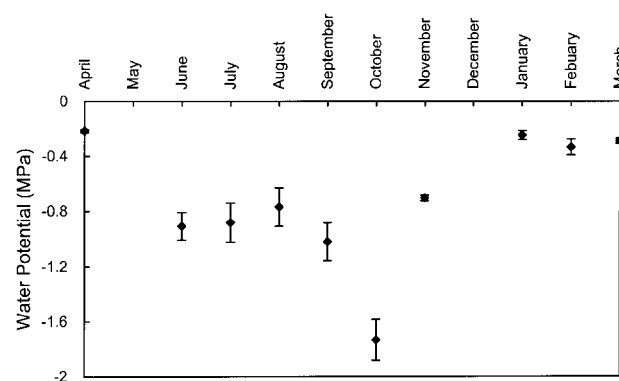


Figure 2. Predawn leaf water potential during 1994 demonstrating the decline in soil water availability over the dry season. Data are mean responses of five species, representing an average community response.

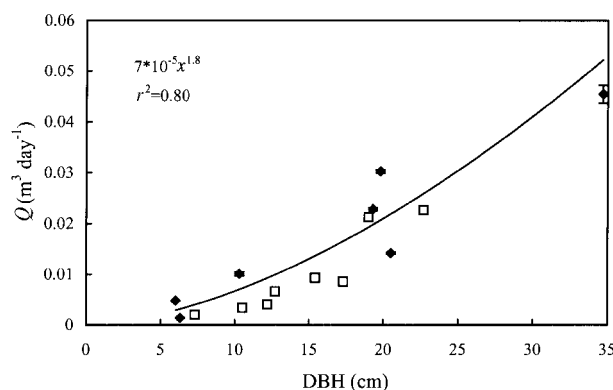


Figure 3. Relationships between mean daily flux ($\text{m}^3 \text{ day}^{-1} \pm \text{SE}$) and DBH (cm) for *E. miniata* (\square) and *E. tetrodonta* (\blacklozenge) in August 1995.

potential and soil water availability throughout the day and concomitant stomatal control of transpiration (Figure 6).

Seasonal responses

Hysteresis was observed in both wet and dry seasons; however, the degree of hysteresis (the area inside the hysteresis loop) was larger during the dry season than during the wet season (Figure 6, ANOVA_{Season}: $F = 6.37$, $\text{df} = 1, 24$, $P < 0.05$), probably because of declining soil water availability. The overall mean difference in the wet season was $0.00059 \text{ m}^3 \text{ day}^{-1} \text{ m}^{-2}$ compared with $0.00134 \text{ m}^3 \text{ day}^{-1} \text{ m}^{-2}$ in the dry season.

There was a marked seasonal response in hourly Q_1 to VPD. Generally for a given VPD, Q_1 was larger during the dry season than during the wet season. In addition, compared with the wet season, the range of VPDs experienced during the dry season was much larger (Figure 1a), and leaves experienced higher values of VPD for most of the day. Consequently Q_1 was higher in the dry season than in the wet season (ANOVA_{Season}: $F = 8.54$, $\text{df} = 1, 24$, $P < 0.05$).

Over the three-year study, mean water use was $0.0097 \text{ m}^3 \text{ day}^{-1} \text{ m}^{-2}$ for the dry season and $0.0049 \text{ m}^3 \text{ day}^{-1} \text{ m}^{-2}$ for the

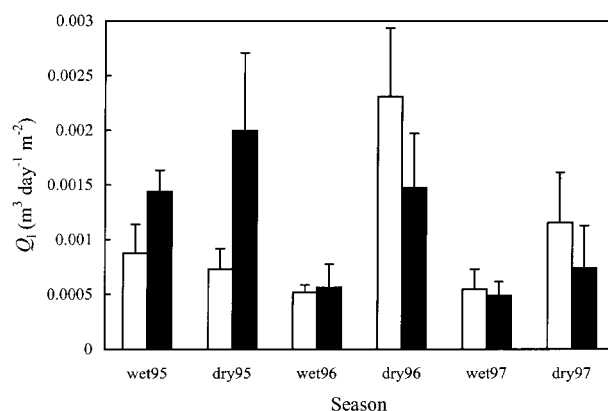


Figure 4. Mean daily transpiration rates ($\text{m}^3 \text{ day}^{-1} \text{ m}^{-2} \pm \text{SE}$) for *E. miniata* (open bars) and *E. tetrodonta* (filled bars) during the wet and dry seasons over the period 1995–1997.

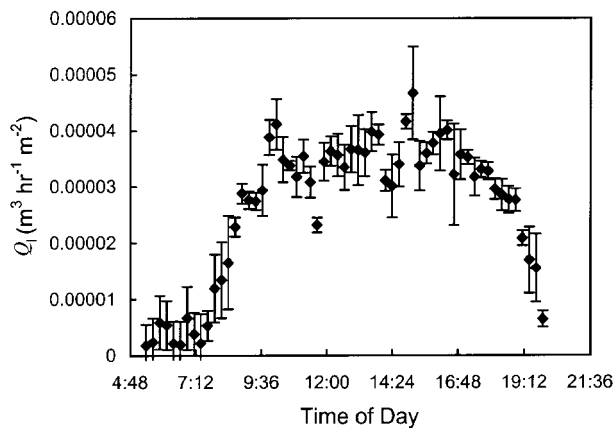


Figure 5. Diurnal pattern of tree transpiration for *E. miniata* in March 1997. Values represent the mean hourly transpiration rate (\pm SE) over the course of the day. Tree DBH was 23.8 cm and leaf area was 52.85 m.

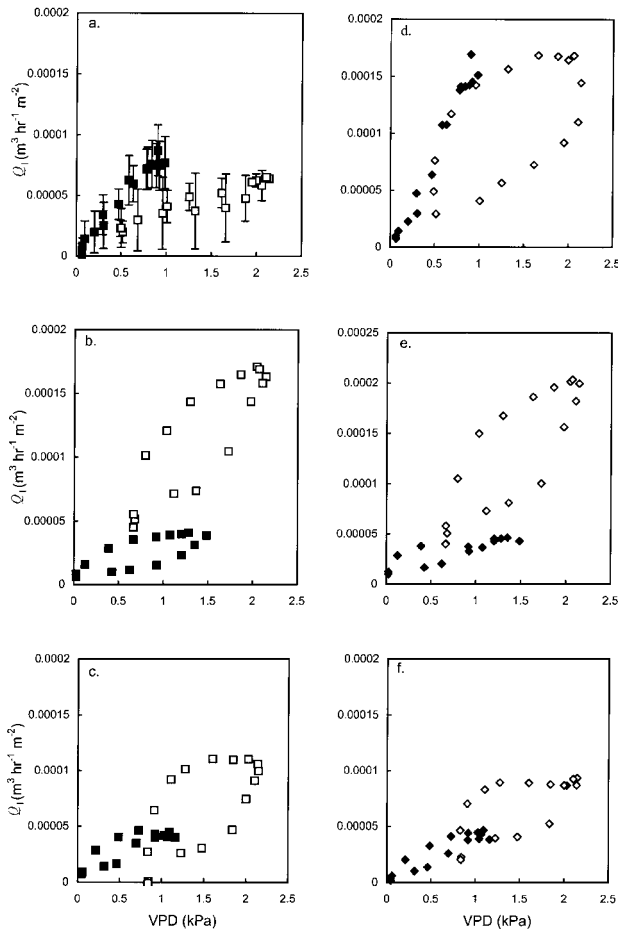


Figure 6. Examples of diurnal pattern of hysteresis in the relationship between transpiration and vapor pressure deficit for *E. miniata* (a–c) and *E. tetrodonta* (d–f) during the wet season (■) and dry season (□). Data shown are from 1995 (top), 1996 (middle) and 1997 (bottom). Representative standard errors are shown in Panel a only.

wet season, indicating that dry-season Q_1 was almost double that of wet-season Q_1 (Figure 7).

Spatial variation of transpiration rate

Transpiration rates were examined at three locations, (six sites) within the catchment area to examine the spatial variability in transpiration within the *E. miniata*–*E. tetrodonta* open forests. There were no significant differences between species, locations, or within locations, between sites. Examination of the mean square estimates suggests that tree-to-tree variability represented the major source of variation in the analysis. Mean Q_1 for each species at each site is shown in Table 1.

Discussion

We examined temporal and spatial variability in the transpiration rates of the two dominant savanna species: (1) to gain a better understanding of this process in north Australian savannas; (2) to investigate the interaction of whole-tree transpiration and climate; and (3) to provide boundary conditions for evapotranspiration and hydrological models operating at the catchment scale.

Daily and seasonal transpiration rates

The climate of the study area shows marked seasonality in rainfall, pan evaporation and VPDs. For the majority of tree species occurring in the area, leaf-scale studies have shown that assimilation rates and stomatal conductances are higher in the morning than in the afternoon, especially in the dry season and stomatal conductances and assimilation rates are higher in the wet season and decline during the dry season in response to increasing VPDs and declining soil water contents (Fordyce et al. 1997, Myers et al. 1997, Eamus and Cole 1997, Prior et al. 1997a, 1997b). However, such patterns were not evident at the tree scale. Transpiration rates increased rapidly throughout the morning in response to increasing radiation, and VPDs and reached a maximum rate by early afternoon, declining toward dusk. A slight midday depression in transpiration was ob-

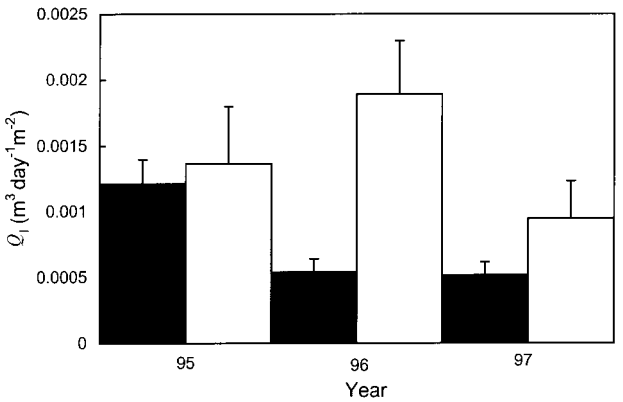


Figure 7. Seasonal tree transpiration rates ($\text{m}^3 \text{ day}^{-1} \text{ m}^{-2} + \text{SE}$) for the wet season (filled bars) and dry season (open bars) during the years 1995–1997 inclusive.

Table 1. Mean transpiration rates, Q_1 , ($\text{m}^3 \text{ day}^{-1} \text{ m}^{-2} \pm \text{SE}$) of the two eucalypts at three locations within the catchment area during the dry season (August 97). Tree-to-tree variability in Q_1 was the major source of variation within the catchment area.

Location	Site	<i>E. miniata</i>	<i>E. tetradonta</i>
1	1	0.0016 ± 0.0004	0.0016 ± 0.0002
	2	0.0015 ± 0.0001	0.0009 ± 0.0001
2	1	0.0012 ± 0.0001	0.0017 ± 0.0002
	2	0.0013 ± 0.0001	0.0007 ± 0.0001
3	1	0.0010 ± 0.00003	0.0008 ± 0.0002
	2	0.0008 ± 0.0001	0.0008 ± 0.0001

served in some of the smaller trees, perhaps representing stomatal control of transpiration as leaf water potentials declined through the morning (Myers et al. 1997).

Transpiration rates were higher during the dry season than during the wet season. This result was contrary to expectations given the extended seasonal drought, and the decline in leaf stomatal conductance and predawn leaf water potential observed in many species within the area (Fordyce et al. 1997, Myers et al. 1997, Prior et al. 1997a, 1997b). The higher Q_1 in the dry season compared with the wet season suggests that soil water availability did not become limiting during the extended dry season. Cook et al. (1998) found that there was sufficient soil water in the upper profile to maintain transpiration rates over the dry season. Increased evaporative demand over the dry season (Figure 1a) was larger than the magnitude of the decline in stomatal conductance resulting from increased VPD and reduced predawn leaf water potential (Prior et al. 1997a, 1997b). This finding highlights the difficulties of extrapolating results at the leaf-scale (for example, reduced stomatal conductance in the dry season) to larger scales such as whole-tree or stand responses. Jarvis (1993) found that, in trees in aerodynamically rough forests, which are well coupled to the atmosphere, and not limited by soil water availability, transpiration will continue at the rate imposed by VPD. This appears to be the case in the *E. miniata*–*E. tetradonta* open forests studied here.

Hysteresis

Hysteresis was observed in the relationship between hourly Q_1 and VPD, and the degree of hysteresis was larger in the dry season than in the wet season. Kelliher et al. (1992) also observed hysteresis in the relationship between sap flux density and air saturation deficit and attributed this to the development of water stress over the day. Eamus and Cole (1997), Prior et al. (1997a) and Fordyce et al. (1997) reported that leaf stomatal conductance and assimilation rates were always higher in the morning than in the afternoon and higher in the wet season than in the dry season (Eamus and Cole 1997). Prior et al. (1997a) found that stomatal conductance was more sensitive to VPD at moderate predawn water potentials, i.e., those experienced throughout most of the dry season (–0.5 to –1.5 MPa) than when predawn water potentials were high (> –0.5 MPa). Duff et al. (1997) reported that the decline in

predawn leaf water potentials in several species at a similar site near to ours coincided with decreasing soil water availability and increasing VPD during the dry season. Doley (1967) observed hysteresis in the relationship between sapflux and leaf water potential in *E. marginata* J. Donn ex Sm. trees of southwest Western Australia and concluded that the principle cause of this hysteresis was resistance to transport of water within the plant and soil. It is also possible that water stored in the stem supplements morning transpiration rates and that this contribution declines in the afternoon (Waring and Running 1978, Waring et al. 1979) and is recharged at night.

Soils in the study area are saturated during the wet season, and although soil water availability may not become limiting during the dry season (Cook et al. 1998), extraction of soil water becomes more difficult, resulting in a larger degree of hysteresis. Stomatal conductance declines in many species in response to increased VPD (Eamus and Cole 1997, Prior et al. 1997a, 1997b) and feed forward responses have been demonstrated where the reduction in stomatal conductance is sufficient to decrease transpiration in response to increasing VPD (Schultz et al. 1972, Thomas and Eamus 1999). Therefore, it is likely that the basis of the hysteresis observed in the present study lies in the stomatal response to VPD and resistance to flow within the plant and soil.

Scaling

Daily tree water use was strongly correlated with DBH and leaf area (cf. Calder et al. 1992, Hatton et al. 1995, Vertessy et al. 1997). Diameter at breast height was the best parameter with which to scale transpiration rate, given the accuracy and ease of measurement compared to leaf area (Calder et al. 1992, Calder 1996). Although the Adelaide Technique can be a reliable estimator of leaf area (Andrew et al. 1979, Hatton and Wu 1995, O'Grady in preparation), accurate estimates of tree leaf area can be obtained only by harvesting, a destructive and time-consuming method.

The relationships between tree water use, DBH and leaf area were similar for the two eucalypts. Hatton et al. (1998) found that leaf water efficiencies within a site were similar for all species at several sites in Australia, and Cook et al. (1998) used relationships derived from five species to scale tree water use to stand water use at a savanna site nearby. This was an important finding because these two eucalypts play the major role in the water balance of the site. It also indicated that scaling tree water use to stand water use in the mixed open forest of northern Australia is valid provided that variability among species is negligible. However, care must be taken when scaling tree water use from a limited sample of trees to plot or stand water use (Hatton and Wu 1995).

Scaled transpiration rates were approximately 1 mm day^{-1} and are within the range reported for eucalypts growing under natural conditions elsewhere in Australia (Dunn and Connor 1993, Farrington et al. 1994, Hatton et al. 1995, Vertessy et al. 1995). Preliminary scaling of tree water use to stand water use suggests that, on an aerial basis, there is little seasonality in tree water use with values ranging from 0.8 to 1.1 mm day^{-1} (O'Grady unpublished data). During the dry season, eva-

potranspiration is dominated by the two eucalypts; however, during the wet season, deciduous and semi-deciduous components of the forest contribute significantly to total transpiration. O'Grady (unpublished data) has demonstrated a 40–50% decline in total (over- and understory) leaf area index of these forests over the dry season. The magnitude of the increase in transpiration per unit leaf area in the dry season is almost equal to the decrease in leaf area index during the dry season, suggesting a causal link between the two. Thus, on an aerial basis, stand water use varies little between seasons because the increase in evaporative demand is equal and opposite to the decline in leaf area per tree.

If physiological studies based on leaf or individual tree responses are to make a contribution to water resource management, processes such as tree water use need to be scaled in space and time. This can be achieved with models that operate at a range of scales from catchment to regional levels. In this study, there were no significant differences in transpiration rates measured in the two eucalypts across the catchment area. A significant proportion of the variance within the data set was attributed to tree-to-tree variability. The tight relationship between transpiration and leaf area or DBH exhibited for both species suggests that the major determinants of spatial variability in stand water use are basal area and leaf area index. Extrapolation of tree water use estimates across the catchment area must take account of heterogeneity in vegetation structure and composition both within and between the vegetation communities within the catchment area (Dunin 1991, Li and Avisar 1994), and the impact of these structural changes on the complex set of nonlinear feedbacks between the land surface and lower atmosphere (Avisar 1995).

Despite declines in leaf stomatal conductance and predawn leaf water potentials during the dry season, Q_1 was higher in the dry season than in the wet season, suggesting that trees had access to sufficient water throughout the year. Transpiration rates exhibited a marked hysteresis in response to VPD and this was larger during the dry season than during the wet season. High VPDs during the dry season were responsible for the increase in Q_1 over the dry season. Tight relationships between tree water use and parameters such as DBH and leaf area, as well as the lack of differences between species suggest that our results can be extrapolated to stand and community levels.

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