

# Does leaf water efficiency vary among eucalypts in water-limited environments?

TOM HATTON,<sup>1</sup> PETER REECE,<sup>2</sup> PETER TAYLOR<sup>3</sup> and KERRY MCEWAN<sup>4</sup>

<sup>1</sup> CSIRO Land and Water, Private Bag, Wembley, Western Australia 6014, Australia

<sup>2</sup> CSIRO Land and Water, GPO Box 1666 Canberra, ACT 2600, Australia

<sup>3</sup> Department of Agronomy and Farming Systems, University of Adelaide, Roseworthy Campus, Roseworthy, South Australia 5371, Australia

<sup>4</sup> CSIRO Land and Water, Private Bag No. 2, Glen Osmond, South Australia 5064, Australia

Received July 24, 1997

**Summary** There is a need to generalize water use behavior of eucalypts to facilitate bioengineering and landscape remediation programs in a wide range of Australian environments. A critical question can be stated as a null hypothesis: tree water use per unit leaf area (leaf efficiency) is independent of eucalypt species. This is implicitly equivalent to the hydrological equilibrium hypothesis that states that leaf area is a function of climate, at least in cases where transpiration and growth are limited by soil water. Failure to reject this null hypothesis simplifies (a) the selection of tree species for water balance management, (b) the generation of regional-scale expectations of leaf area index, and (c) the estimation (monitoring) of the effectiveness of plantations in controlling site water balance. The hypothesis was tested with tree water use data collected in natural multi-species stands across Australia, including sites in the wet–dry season tropical woodlands of the Northern Territory, the Mediterranean climate forests of Western Australia, and a woodland system in southern New South Wales receiving an even distribution of rainfall throughout the year. We also tested the hypothesis in a multi-species tree plantation growing on a saline gradient.

In each case, we could not reject the hypothesis of constant leaf efficiency among eucalypts. In every case there was a common, strong, linear relationship among tree leaf area and mean daily water use by all tree species in a sample. Single factor (species) analysis of variance did not detect significant differences between leaf water efficiencies of species. For the jarrah forest (*Eucalyptus marginata* J. Donn ex Sm., *E. calophylla* R. Br. ex Lindl.), the null hypothesis held in both spring (wet) and autumn (dry) conditions. The null hypothesis held in the mixed species woodland of New South Wales (*E. macrorhynca* F.J. Muell. ex Benth., *E. blakelyi* Maiden., *E. polyanthemus* Schauer.) under summer and autumn conditions, and across five species in the wet–dry tropical woodland (*E. miniata* A. Cunn. ex Schauer, *E. tetradonta* F.J. Muell., *E. porecta* S.T. Blake, *Erythrophleum chlorostachys* F.J. Muell., and *Terminalia ferdinandiana* Exell.). The null hypothesis also held for a plantation of *E. occidentalis* Endl. and provenances of *E. camaldulensis* Dehnh. growing on a shallow saline gradient; i.e., leaf water efficiency remained constant

across species and varieties despite obvious effects of salinity on the size of individual canopies. We conclude that there is little evidence for rejecting the hypothesis that leaf efficiency does not vary significantly among sympatric eucalypt species in rainfall-limited (soil-water-limited) systems. These findings open the way for useful bioengineering generalities about the hydrological role of trees in the Australian landscape.

**Keywords:** bioengineering, *Eucalyptus*, hydrological equilibrium theory, landscape remediation, leaf efficiency, Mediterranean climate, salinity, tropical forest.

## Introduction

A knowledge of how vegetation, in particular trees in the genus *Eucalyptus*, affects local and regional water balances in Australia is necessary to provide a basis for selecting species for revegetation and for specifying the location and extent of plantations to achieve a stated hydrological aim (Morris and Thompson 1983). Many studies on the water relations of Australian evergreen plants have been undertaken to obtain this information. However, these studies have been made at a range of scales and with diverse experimental approaches, and consequently have produced a confusing picture of how transpiration varies among species and sites.

At the leaf scale, porometric studies of eucalypt transpiration often show differences in leaf conductance among species. In the most ambitious of these studies (Hookey et al. 1987), significant differences were found among eucalypt species growing over a shallow saline groundwater system, with some species estimated to transpire (based on scaled stomatal conductances) at three to four times the rate of other species at the end of summer. However, it is difficult to extrapolate leaf-level data to the long-term behavior of tree canopies in established stands, because of the variability of leaf-scale conductance measurements in both time (Turner 1991) and space (Jarvis et al. 1981) and the inappropriate translation of measured conductances into transpiration (Denmead 1984, Meinzer 1993). Nevertheless, these leaf scale studies have led to the paradigm of a dominant role for stomata in regulating transpiration, and

the existence of large differences in stomatal conductance (and hence transpiration rates) among eucalypts and other tree species.

At the stand scale, a different paradigm has emerged based on micrometeorological, climatological and hydrological investigations. When different forest systems within the same region are compared on the basis of their annual evapotranspiration, differences are often small (Aussenac 1972, Dunin and Mackay 1982, Roberts 1983, Pomeroy et al. 1988). Furthermore, ecohydrological studies at the regional scale suggest that there are broad consistencies in the rainfall–leaf area index (LAI) relationship across plant communities. Specht (1972) hypothesized that the structure of canopies was influenced by the availability of soil water, and demonstrated that the LAIs of diverse Australian evergreen plant communities were strongly and similarly related to a climatic index of evaporative demand and rainfall (Specht and Specht 1989). Hatton et al. (1997a) cited this work as evidence in support of Eagleson's optimality hypothesis of an ecohydrological equilibrium (Eagleson 1982, Eagleson and Tellers 1982, Eagleson and Segarra 1985). Other authors have established an empirical relationship between site LAI and available soil water for evergreen vegetation at regional scales (Grier and Running 1977, Gholz 1982, Nemani and Running 1989, Pierce et al. 1993). These observations imply that leaf efficiency (amount of water transpired per unit area of leaf; cf. Greenwood et al. 1985, Hatton and Wu 1995) is constant across evergreen species *assemblages* in water-limited environments.

To reconcile differences in plant water relations (conductance) among eucalypt species at the leaf scale, with strong similarities in leaf efficiency at the regional scale, Meinzer (1993) explained differences in transpiration across these scales in terms of the varying role of boundary layer conductance (cf. Jarvis and McNaughton 1986, McNaughton and Jarvis 1991), but also recognized adjustments in leaf area that may compensate for plant water stress.

Techniques exist at an intermediate scale that can help resolve the question of differences in leaf efficiency among species. A variety of thermoelectric and tracer techniques have been developed that can measure transpiration of individual trees (Marshall 1958, Cohen et al. 1981, Edwards and Warwick 1984, Granier 1985, Calder et al. 1986, Baker and van Bavel 1987, Ěermák and Kuèera 1987, Hatton et al. 1995), allowing the integration of stomatal and boundary layer conductance behaviors in space and time. Such studies indicate that transpiration scales linearly and strongly with tree leaf area (Greenwood et al. 1985, Ěermák and Kuèera 1987, Werk et al. 1988, Vertessy et al. 1994, Hatton et al. 1995), although under very dry conditions this relationship may become curvilinear (Greenwood et al. 1982, Hatton and Wu 1995). A corollary of this linearity between tree leaf area and transpiration within a stand is the constancy of leaf efficiency among trees of different sizes within a species, including *Eucalyptus* spp. However, it is not known if leaf efficiency remains constant among eucalypt species growing together in the same stand. That is, do individual trees of sympatric species have similar leaf efficiencies when subjected to periodic water stress, or do different *Eucalyptus* species, when faced with the same supply

of water and demand by the atmosphere, come to unique solutions to optimize the balance between stomatal conductance and leaf area. To distinguish between these possibilities, we tested the hypothesis that leaf efficiency does not vary among eucalypt species growing together under similar conditions at sites with seasonal water limitations.

We examined the constancy of leaf efficiency with datasets of tree water use and leaf area collected in multi-species eucalypt stands growing in (a) a partially cleared temperate woodland site with an even distribution of monthly rainfall, (b) a natural forest subject to a long summer dry season, and (c) a natural woodland in the wet–dry tropics. We also examined leaf efficiencies of eucalypts growing in an experimental plantation on a local saline gradient in a semi-arid climate.

## Methods

### *Tree water use*

Tree water use was measured by the heat pulse method with Greenspan Technology Sapflow Sensors (Warwick, Australia). The sampling and numerical techniques associated with this application have been described by Hatton et al. (1995). In each case, sap flow was logged simultaneously for all trees in the sample on a 20–30 min basis, throughout the sampling period. Determination of sampling depths in the sapwood and the integration of point estimates of velocity were carried out as described by Hatton et al. (1990). Wound effects were corrected for by Swanson and Whitfield's (1981) numerical approach. Wound diameters were estimated by inspection of the region surrounding the probes. Previous studies of wound development in eucalypts (Moore 1993, Hatton et al. 1995) showed good correspondence between the extent of discoloration of the probe region and tylose formation as estimated from light and scanning electron microscopy. Wound diameters varied between 2.2 and 2.8 mm (cf. Olbrich 1991, Dunn and Connor 1993, Barrett et al. 1995). Wood and water contents were obtained as described by Hatton and Vertessy (1990). The inner boundary of sapwood (conducting wood) was determined by incremental measurement of sap flow with depth (Hatton et al. 1995). Although sensitivity analyses of the heat pulse technique show that the potential error can be as high as 38% (Hatton et al. 1995), tests of the heat pulse method against known transpiration rate generally show an accuracy of 7–15% (Olbrich 1991, Dunn and Connor 1993, Barrett et al. 1995, Hatton et al. 1995). Results were expressed as mean water use per day for each tree over the monitored period.

### *Leaf area estimation*

In every case, leaf area was measured by the Adelaide (module) technique described by Andrew et al. (1979). Two independent observers estimated the number of eucalypt modules for each monitored tree; the mean of these two estimates was converted to tree leaf area on the basis of the leaf area of a standard module for each species as measured by electronic planimetry (Hatton et al. 1995). This approach is effectively the same as applied by Carbon et al. (1979) to the same jarrah forest reported herein. Hatton et al. (1995) tested this method

against four trees of varying sizes and of known leaf area (determined by destructive sampling of whole-tree canopies); linear regression (forced through the origin) of the mean estimated values against known leaf areas yielded a slope of 1.13 ( $r^2 = 0.96$ ). In this study, bias between the observers was less than 10% in all cases at all sites. All of the tree leaf areas reported were estimated by the same pair of observers.

#### Sites and sampling

**Mixed species woodland** The grazed and partially cleared mixed eucalypt woodland site near Goulburn, New South Wales (34°41' S, 149°56' E) has been described in detail by Kalma and Jupp (1990). The climate at this site is temperate, with a mean annual rainfall of 679 mm with no distinct seasonality. Potential evaporation exceeds rainfall for over half of the year. Tree LAI at the landscape scale is less than one, and individual tree canopies are quite open. Over the period December 8–18, 1992, when the soil was near field capacity, two trees of *Eucalyptus polyanthemos* Schauer. and one tree of *E. blakelyi* Maiden. were monitored for transpiration. Over the period March 12–25, 1993, when soil water was relatively high, one *E. macrorhynca* F.J. Muell. ex Benth. tree was added to the set of trees monitored. These data were originally reported in Hatton and Wu (1995).

**Jarrah forest** The jarrah forest of southwestern Australia grows where rainfall exceeds 650 mm per year, but develops into a relatively tall (30–40 m) forest despite a prolonged summer drought resulting from a Mediterranean rainfall distribution. This is a result of the maintenance of relatively high rates of transpiration through much of the dry season by extraction of water from deep (> 20 m) in the soil profile (Carbon et al. 1980, 1981a, 1981b, Colquhoun et al. 1984). Tree water use was studied at a site (32°20' S, 116°05' E) in the Gordon Catchment, in a high rainfall zone (1050 mm) of the forest. This site is in a 50-year-old stand with an LAI varying between 1.0 and 1.5, and is maintained by ALCOA Pty. Ltd. as part of a research program on jarrah forest management. Tree water use was monitored over the period October 6–16, 1993 in four jarrah (*E. marginata* J. Donn ex Smith) and three marri (*E. calophylla* R.Br. ex Lindl.) trees; at this time surface soil water was high following winter rains. Water use was later monitored in four jarrah and four marri trees over the period March 10–17, 1994, when soil water was relatively low after a dry summer.

**Tropical woodland** The tropical woodland site is near the Howard River east of Darwin in the Northern Territory (12°30' S, 131°06' E). The climate is wet-dry tropical, with mean annual rainfall of 1600 mm, almost exclusively between October and March (summer). Tree LAI rarely exceeds 1.5. There is evidence that the woodland persists through the long dry season through access to groundwater in a shallow, unconfined aquifer system, but water stress nevertheless develops toward September (Pidsley et al. 1994). At the end of the wet season, tree water use was monitored over the period April 15–20, 1994, in five *E. miniata* A. Cunn. ex Schauer, four *E. tetradonta* F.J. Muell., one *E. porecta* S.T. Blake, two *Erythrophleum chlorostachys* (F.J. Muell.) Baillon and two

*Terminalia ferdinandiana* Exell. trees; the latter species is of a dry season deciduous nature. Toward the end of the dry season (September 3–9, 1994), four *E. miniata*, four *E. tetradonta*, two *E. porecta*, and two *Erythrophleum chlorostachys* were monitored.

**Saline plantation site** A small (30 × 100 m) experimental plantation was established in 1986 on a sloping edge of a saline lake on the Yorke Peninsula (34°45' S, 137°40' E) by Primary Industries South Australia. Annual rainfall at the site is approximately 450 mm, mostly in winter. Groundwater at this site is shallow (0.5–2 m below ground level) and quite saline (over 60 dS m<sup>-1</sup>). The trees included *E. occidentalis* Endl., *E. camaldulensis* Dehnh. (local provenance) and *E. camaldulensis* (provenance: Lake Albacutya). The latter variety has been touted as superior for plantations on shallow saline watertables (e.g., Moreshet 1981). The plantation was laid out to assess performance of tree varieties with distance from the saline lake, equivalent to a gradient in depth to the saline water table. Although most trees established and initially grew, after eight years the impact of proximity to saline groundwater was obvious. There is a clear gradient in size with distance from the lake (Figure 1), and the canopies of trees near the lake are now dying back (or dead) as salt accumulates in their (shallow) root zone. Over the period October 17–24, 1996, we monitored water use of three *E. occidentalis*, four *E. camaldulensis* (local provenance) and six *E. camaldulensis* (provenance: Lake Albacutya) trees. This measurement was selected so that soil matric potentials would be low against the background of the osmotic gradient, and atmospheric demand would be significant following winter.

For each case, tree water use was regressed on tree leaf area, using a first-order regression model and assuming the independent variable was measured without error. In addition, a one-way analysis of variance was performed where the treatment was the species or provenance and replication was at the tree level. No attempt was made to block out other (spatial)

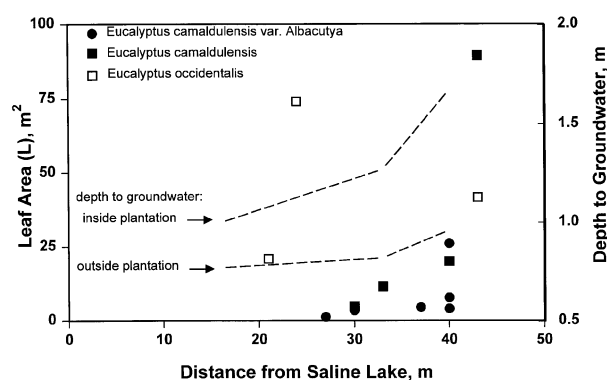


Figure 1. Tree leaf area with distance from the edge of a saline lake, and depth to a saline groundwater table, for an experimental plantation of eucalypts on the Yorke peninsula, South Australia. Note the general trend for larger canopies with deeper water tables and distance from the lake edge, particularly for the two varieties of *E. camaldulensis*. Trees of *E. occidentalis* grew relatively large in relation to the salinity gradient.

sources of variation because of resource limitations.

## Results

There was little observation bias on leaf area between the two observers. For the jarrah forest in October 1994, the linear regression between the estimates of leaf area by the two observers had a nonsignificant intercept ( $-0.31 \text{ m}^2$ ,  $P > 0.2$ ) and a slope of 1.06 ( $r^2 = 0.97$ ,  $df = 6$ ). For the tropical woodland in April 1994, the linear regression between the observers' estimates had a nonsignificant intercept ( $0.02 \text{ m}^2$ ,  $P > 0.2$ ) and a slope of 1.00 ( $r^2 = 0.94$ ,  $df = 12$ ). In the case of the saline plantation, the linear regression between the two observers' estimates for the entire plantation ( $n = 101$  trees) had a statistically nonsignificant  $y$ -intercept of  $-0.05$  ( $P > 0.2$ ) and a slope of 1.035 ( $r^2 = 0.99$ ) over a leaf area ranging from 0.05 to 74  $\text{m}^2$ .

Large seasonal variation existed in the slopes of the leaf area–tree water use relationship at a given site. At the mixed woodland site, the values for December and March were 1.08 and 1.59, respectively; soil water was relatively high at both times, but vapor pressure deficits for December were uncharacteristically low (Guerra 1995). The slopes of this relationship for the jarrah forest in spring and summer were 3.80 and 3.26, respectively. Vapor pressure deficits were much higher during the summer measurements than during the spring measurements (Silberstein 1996), but soil water was limiting in summer. The eucalypt leaf area–tree water use relationships for the wet and dry seasons in the tropical woodland had slopes of 2.45 and 0.86, respectively. Although vapor pressure deficits were higher in the dry season, evapotranspiration declined over this period from 0.91 of equilibrium evaporation to 0.35 of equilibrium as a result of limited soil water (Hatton et al. 1997b).

There was no significant difference in leaf efficiency among the eucalypt species examined at any site for any sampling period (Table 1). In the case of the tropical woodland, there was a significant difference in leaf efficiency ( $P < 0.05$ ) between the eucalypts and non-eucalypts, including *Terminalia*, in the wet season. There was no significant difference in leaf efficiency between the eucalypts and *Erythrophleum chlorostachys* in the dry season ( $P > 0.20$ ). None of the  $y$ -intercepts of the regressions of leaf efficiency and mean daily transpiration was significantly different from zero ( $P > 0.05$ ) (Figures 2–8). The slopes of these regressions ranged between 0.86 and 3.80.

Table 1. Results of ANOVA for the null hypothesis that leaf efficiency does not vary among *Eucalyptus* species. Note that there were too few observations on the mixed woodland for this analysis. The  $P$ -value is probability of Type I error.

Site	Date	$F$ -statistic	$P$ -value
Jarrah forest	October 1993	6.61	0.20
Jarrah forest	March 1994	5.99	0.20
Tropical woodland	April 1994	3.71	0.20
Tropical woodland	September 1994	4.07	0.20
Saline plantation	October 1996	4.10	0.20

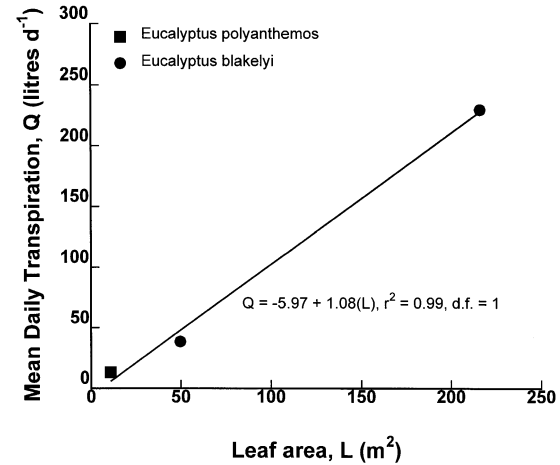


Figure 2. Tree leaf area versus mean daily transpiration for a mixed species woodland in New South Wales measured December 8–18, 1992.

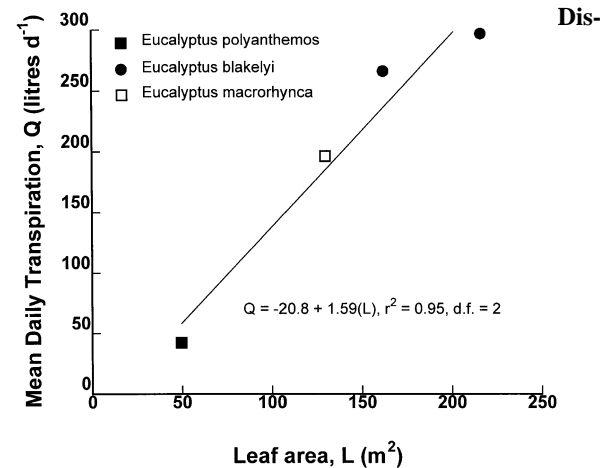


Figure 3. Tree leaf area versus mean daily transpiration for a mixed species woodland in New South Wales measured March 12–25, 1993.

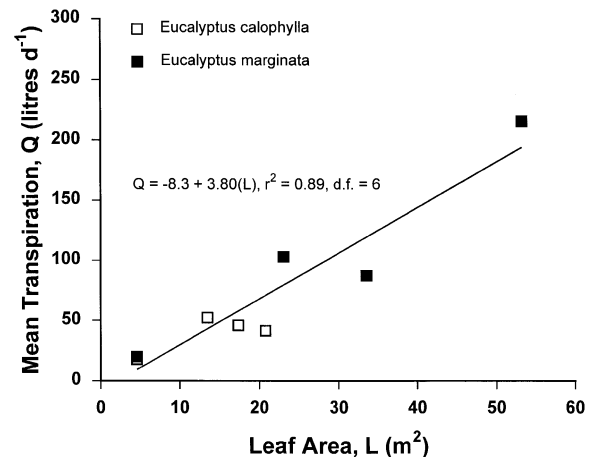


Figure 4. Tree leaf area versus mean daily transpiration for a jarrah forest in Western Australia measured October 6–16, 1993.

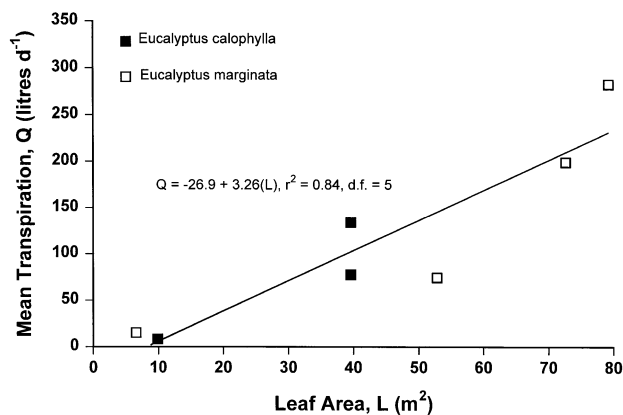


Figure 5. Tree leaf area versus mean daily transpiration for a jarrah forest in Western Australia measured March 10–17, 1994.

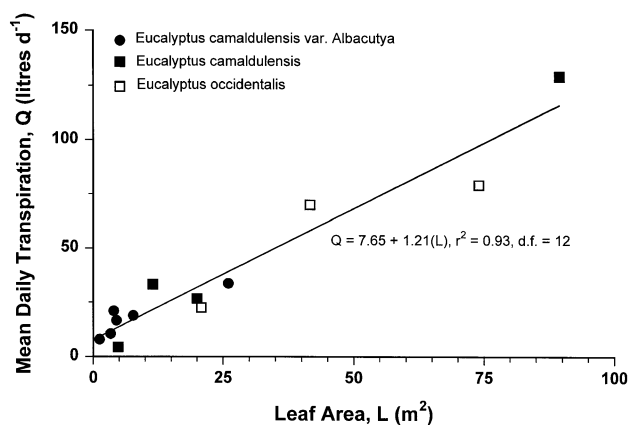


Figure 8. Tree leaf area versus mean daily transpiration for a plantation growing on a saline groundwater gradient in South Australia measured October 17–24, 1996.

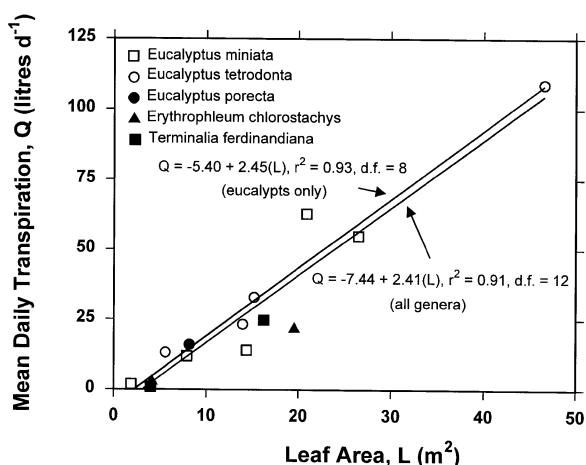


Figure 6. Tree leaf area versus mean daily transpiration for tropical woodland in the Northern Territory measured April 15–20, 1994. Regressions with and without non-eucalypt species.

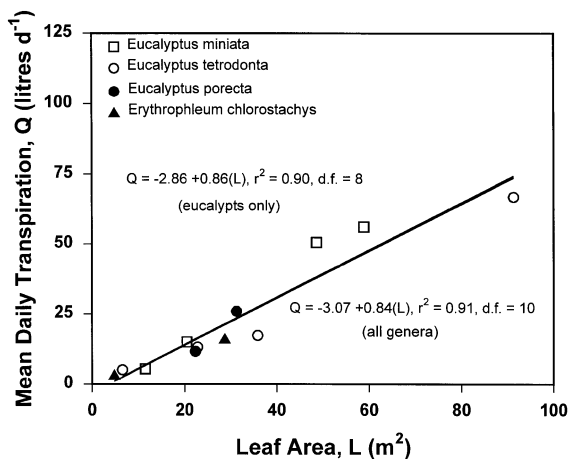


Figure 7. Tree leaf area versus mean daily transpiration for a tropical woodland in the Northern Territory measured September 3–9, 1994. Regressions with and without non-eucalypt species.

## Discussion

We could not reject the null hypothesis that leaf efficiency does not vary among eucalypts in environments subjected to seasonal water limitations. We note, however, that the results from the mixed species woodland (Figures 2 and 3) are based on few data. The measurement errors, on the order of 10% for both leaf area and transpiration, are large enough to mask ecologically and physiologically significant differences. Further, we recognize the lack of spatial replication in this set of studies of diverse Australian forests, although we have repeated the measurements over time in most cases. The strength of our inference about eucalypt leaf efficiencies lies in the similarity of results for different sets of species across widely varying climates and landscapes.

Leaf-scale studies in the jarrah forest (Carbon et al. 1981a) indicated little difference in leaf efficiency (or plant water potential) between native *E. marginata* and a 6–8-year-old plantation *E. microcorys* F.J. Muell. growing nearby in the wet season (winter), but found slightly higher values of leaf efficiency for the native forest in summer than for the plantation trees. However, they did not scale these results to the whole canopy, and the plantation had a higher LAI than the natural forest. Carbon et al. (1981b) found little difference between the transpiration responses of *E. marginata* and *E. calophylla* growing at the same site. Colquhoun et al. (1984) compared leaf-scale conductance and xylem water potential of these two species and found similar transpiration responses.

Few comparative studies of eucalypt leaf efficiency have been made at the stand or plantation scale, and most of these relied on either ventilated chambers or site water balances, and in many cases were done on young plantations that may not have come into hydrologic equilibrium with rainfall. The results of some studies employing whole-tree ventilated chambers tend to corroborate our null hypothesis (e.g., Greenwood et al. 1985). However, using this same technique, Greenwood and Beresford (1979) found species differences in leaf efficiencies among young (1–2 years old) plantation trees, but pointed out that some of these trees may have gained access to a local

groundwater table.

Honeysett et al. (1992) examined the water balance of fertilized 4–5-year-old plantations of *E. delegatensis* and *E. nitens* at a site naturally supporting wet sclerophyll forest (annual rainfall 916–1132 mm during study). Soil water content was monitored to a depth of 1.2 m. These authors found evidence that, at least during the measurement period, deep drainage had ceased, but they did not quantify soil evaporation or runoff. Although the LAI of *E. nitens* was approximately twice that of *E. delegatensis*, the species used only 7% more water. This result would seem to contradict our null hypothesis, unless (a) the site was not water stressed (potential evaporation at this site is probably not much more than 1100 mm year<sup>-1</sup>), (b) the experimental approach could not accurately isolate the transpiration component of the water balances of these plantations, or (c) the leaf areas were not yet in equilibrium with rainfall.

The hypothesis that evergreen vegetation will adjust its LAI in response to long-term water availability (Specht 1972, Grier and Running 1977, Eagleson 1982, Eagleson and Tellers 1982, Gholz 1982, Eagleson and Segarra 1985, Nemani and Running 1989, Pierce et al. 1993, Hatton and Wu 1995) seems compelling. Young plantations may violate this condition if they do not yet fully occupy the site in a hydrological sense, or if they initially use soil water stored in the profile prior to their establishment; however, this is not a consideration in the natural stands we studied. There was evidence that the productivity of the saline plantation had reached its limit because of osmotic constraints on the availability of water.

The saline plantation data were significant in two respects. First, although the effects of salinity on tree growth differed among the species, leaf efficiencies were similar (Figure 8). Thus, despite the observed differences in the growth responses of species to a salinity gradient, tree water use scaled similarly with canopy leaf area across species and provenances within species. Second, the species and provenances included in the saline plantation trial do not occur naturally together. Therefore, in contrast to the other cases examined in this paper, the possibility of equivalent leaf efficiency arising from either recent co-evolution or local co-adaptation is eliminated. Adams (1995) has challenged the dominant paradigm, traced back to Beadle (1954), that nutrients delimit vegetation types and plant development in Australia. Adams argued that water availability is the dominant control on vegetation in geologically old landscapes, because nutrient recycling supplies most of the nitrogen and phosphorus (and other nutrients) required for tree growth in Australian forest and woodlands. If eucalypts have adapted such that nutrients generally do not limit the extent of their canopy development or function to the same degree as does water, then this explanation could account in part for the uniformity of leaf efficiencies among allopatric species.

Cowan (1977, 1978, 1982) linked photosynthesis and stomatal conductance in water-limited environments by hypothesizing an optimal behavior defined by the availability of soil water. He asserted that the mean rate of CO<sub>2</sub> assimilation (*A*) could not be increased without increasing transpiration (*T*) over the same period, and that there is a nonlinear relationship between *A* and *T* that defines the increasing cost to the plant in

terms of water loss as the benefits from assimilation increase, the slope of which is equivalent to the unit marginal cost. Optimization requires that the plant maintains the unit marginal cost uniform in all leaves and constant in time. Although this theory is expressed at the leaf level, Cowan (1982) anticipated its application to the whole plant. If there is a well-defined optimum in photosynthetic capacity and stomatal conductance, then perhaps various species of eucalypts have evolved similar leaf water efficiencies close to that optimum.

Based on the simple model of canopy conductance proposed by Szicz and Long (1969):

$$r_c = \frac{\bar{r}_s}{\text{LAI}},$$

where  $r_c$  is canopy conductance and  $\bar{r}_s$  is mean stomatal resistance, there are two variables controlling transpiration in plants. In water-limited environments, evergreen plants employ both strategies to regulate water use, but adjusting the numerator comes at a price: higher leaf–air vapor pressure gradients, lower net carbon assimilation per unit leaf area, and potentially fatal leaf temperatures (e.g., Pook 1986). Adjustment of LAI can help maintain conductances of the remaining leaves during stressful periods, as has been observed in evergreen plant communities in Australia. Our study provides evidence that sympatric eucalypts maintain a similar balance between leaf area and stomatal conductance.

If our hypothesis of similar leaf efficiencies among eucalypts holds, then the process of selecting species for revegetation work can be simplified. For example, revegetation aimed at water balance control in a seasonally water-limited environment, may be achieved with a fully stocked plantation of any eucalypt species provided that it survives. Further, the possibility that the extent of canopy development can be used as an indicator of hydrological behavior, regardless of eucalypt species, could offer an efficient way of assessing the effectiveness of tree plantations and natural stands in maintaining the landscape water balance.

#### Acknowledgments

The authors thank the owners of “Lockyersleigh,” ALCOA Pty. Ltd., Conservation and Land Management (Western Australia), Department of Land Planning and Environment (Northern Territory), Primary Industries (South Australia) and K. Treloar for providing access to the sites described in this paper and for logistical support in the field. This work was funded by the Joint Venture Agroforestry Program of the Land and Water Resources, Rural Industries, and Forest and Wood Products Research and Development Corporations.

#### References

- Adams, M.A. 1995. Distribution of eucalypts in Australian landscapes: landforms, soils, fire and nutrition. *In* Nutrition of the Eucalypts. Eds. P.M. Attiwill and M.A. Adams, CSIRO, Melbourne, pp 61–76.
- Andrew, M.H., I.R. Noble and R.T. Lange. 1979. A non-destructive method for estimating the weight of forage on shrubs. *Aust. Range J.* 1:225–231.

- Aussenac, G. 1972. Étude de l'évaporation réelle de quatre peuplements forestiers dans l'est de la France. *Ann. Sci. For.* 29:369–389.
- Baker, J.M. and C.H.M. van Bavel. 1987. Measurement of mass flow of water in the stems of herbaceous plants. *Plant Cell Environ.* 10:777–782.
- Barrett, D.J., T.J. Hatton, J.E. Ash and M.C. Ball. 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia. *Plant Cell Environ.* 18:463–469.
- Beadle, N.C.W. 1954. Soil phosphate and the delimitation of plant communities in eastern Australia. *Ecology* 35:370–375.
- Calder, I.R., M.N. Narayanswamy, N.V. Srinivasalu, W.G. Darling and A.J. Lardner. 1986. Investigation into the use of deuterium as a tracer for measuring transpiration from eucalypts. *J. Hydrol.* 84:345–351.
- Carbon, B.A., G.A. Bartle and A.M. Murray. 1979. A method for visual estimation of leaf area. *For. Sci.* 25:53–58.
- Carbon, B.A., G.A. Bartle, A.M. Murray and D.K. MacPherson. 1980. The distribution of root length, and the limits to flow of soil water to roots in a dry sclerophyll forest. *For. Sci.* 4:656–664.
- Carbon, B.A., G.A. Bartle and A.M. Murray. 1981a. Water stress, transpiration and leaf area index in eucalypt plantations in a bauxite mining area in south-western Australia. *Aust. J. Ecol.* 6:459–466.
- Carbon, B.A., G.A. Bartle and A.M. Murray. 1981b. Patterns of water stress and transpiration in jarrah (*Eucalyptus marginata* Donn ex Sm.) forests. *Aust. For. Res.* 11:191–200.
- Ěermák, J. and J. Kučera. 1987. Transpiration of mature stands of spruce (*Picea abies* (L.) Karst.) as estimated by the tree-trunk heat balance method. *In Forest Hydrology and Watershed Management. IAHS-AISH Publ.* 167, pp 311–317.
- Cohen, Y., M. Fuchs and G.C. Green. 1981. Improvement of the heat pulse method for determining the sap flow in trees. *Plant Cell Environ.* 4:391–397.
- Colquhoun, I.J., R.W. Ridge, D.T. Bell, W.A. Loneragon and J. Kuo. 1984. Comparative studies in selected species of *Eucalyptus* used in rehabilitation of the northern jarrah forest, Western Australia. I. Patterns of xylem pressure potential and diffusive resistance of leaves. *Aust. J. Bot.* 32:367–373.
- Cowan, I.R. 1977. Stomatal behavior and environment. *Adv. Bot. Res.* 4:117–228.
- Cowan, I.R. 1978. Water use in higher plants. *In Water, Planets, Plants and People.* Ed. A.K. McIntyre. Australian Academy of Science, Canberra, pp 71–107.
- Cowan, I.R. 1982. Regulation of water use in relation to carbon gain in higher plants. *In Encyclopedia of Plant Physiology*, Vol. 12B. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, Berlin, pp 589–613.
- Denmead, O.T. 1984. Plant physiological methods for studying evapotranspiration: problems of telling the forest from the trees. *Agric. Water Manag.* 8:167–189.
- Dunin, F.X. and S.M. Mackay. 1982. Evaporation of eucalypt and coniferous forest communities. *In The First National Symposium on Forest Hydrology*, I. Eds. E.M. O'Loughlin and L.J. Bren. Institution of Engineers, Australia National Publication No. 82/6, pp 18–25.
- Dunn, G.M. and D.J. Connor. 1993. An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different ages. *Tree Physiol.* 13:321–336.
- Eagleson, P.S. 1982. Ecological optimality in water-limited natural soil-vegetation systems. 1. Theory and hypothesis. *Water Resour. Res.* 18:325–340.
- Eagleson, P.S. and R.I. Segarra. 1985. Water-limited equilibrium of savanna vegetation systems. *Water Resour. Res.* 21:1483–1493.
- Eagleson, P.S. and T.E. Tellers. 1982. Ecological optimality in water-limited natural soil-vegetation systems. 2. Tests and applications. *Water Resour. Res.* 18:341–354.
- Edwards, W.R.N. and N.W.M. Warwick. 1984. Transpiration from a kiwi fruit vine as estimated by the heat pulse technique and the Penman-Monteith equation. *N.Z. J. Agric. Res.* 27:537–543.
- Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63:469–481.
- Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42:193–200.
- Greenwood, E.A.N. and J.D. Beresford. 1979. Evaporation from vegetation in landscapes developing secondary salinity using the ventilated chamber technique. I. Comparative transpiration from juvenile *Eucalyptus* above saline groundwater. *J. Hydrol.* 42:369–382.
- Greenwood, E.A.N., J.D. Beresford, J.R. Bartle and R.J. Barron. 1982. Evaporation from vegetation in landscapes developing secondary salinity using the ventilated chamber technique. II. Evaporation from a regenerating forest of *Eucalyptus wandoo* on land formerly cleared for agriculture. *J. Hydrol.* 58:357–366.
- Greenwood, E.A.N., L. Klein, J.D. Beresford and G.D. Watson. 1985. Differences in annual evaporation between grazed pasture and *Eucalyptus* species growing on a saline farm catchment. *J. Hydrol.* 78:261–278.
- Grier, C.C. and S.W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* 58:893–899.
- Guerra, L.C. 1995. Predicting evapotranspiration and soil moisture distribution from terrain attributes and weather. Ph.D. Thesis, Australian National University, Canberra, 197 p.
- Hatton, T.J. and R.A. Vertessy. 1990. Transpiration of plantation *Pinus radiata* estimated by the heat pulse method and the Bowen ratio. *Hydrol. Proc.* 4:289–298.
- Hatton, T.J. and H. Wu. 1995. Scaling theory to extrapolate individual tree water use to stand water use. *Hydrol. Proc.* 9:527–540.
- Hatton, T.J., E.A. Catchpole and R.A. Vertessy. 1990. Integration of point measures of sapflow velocity to estimate plant water use. *Tree Physiol.* 6:201–209.
- Hatton, T.J., S.J. Moore and P.H. Reece. 1995. Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiol.* 15:219–227.
- Hatton, T.J., G.D. Salvucci and H. Wu. 1997a. Eagleson's optimality theory of an ecohydrological equilibrium: *Quo Vadis?* *Funct. Ecol.* 11:665–674.
- Hatton, T.J., D. Pidsley, A.A. Held, P.H. Reece, D.P. Richardson, E. Kerle and A. O'Grady. 1997b. Hydrological investigation at Howard East, N.T. 1. Eucalypt savanna site: transpiration and evaporation, 1994–1996. CSIRO Land and Water Technical Report 25/97, Adelaide, 31 p.
- Honeysett, J.L., C.L. Beadle and C.R.A. Turnbull. 1992. Evapotranspiration and growth of two contrasting species of eucalypts under non-limiting and limiting water availability. *For. Ecol. Manag.* 50:203–216.
- Hookey, G.R., I.C. Loh and J.R. Bartle. 1987. Water use of eucalypts above saline groundwater. Water Resources Directorate, Water Authority of Western Australia, Report No. WH 32, 40 p.

- Jarvis, P.G., W.R. Edwards and H. Talbot. 1981. Models of plant and crop water use. *In* Mathematics and Plant Physiology. Eds D.A. Rose and D.A. Charles-Edwards. Academic Press, London, pp 151–194.
- Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15:1–49.
- Kalma, J.D. and D.L.B. Jupp. 1990. Estimating evaporation from pasture using infrared thermometry: evaluation of a one-layer resistance model. *Agric. For. Meteorol.* 51:223–246.
- Marshall, D.C. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiol.* 6:385–396.
- McNaughton, K.G. and P.G. Jarvis. 1991. Effects of spatial scale on stomatal control of transpiration. *Agric. For. Meteorol.* 54:279–301.
- Meinzer, F.C. 1993. Stomatal control of transpiration. *Trees* 8:289–294.
- Moore, S.J. 1993. Estimating stand transpiration in a *Eucalyptus populnea* woodland. Honours Thesis, Australian National University, Canberra, 98 p.
- Moreshet, S. 1981. Physiological activity, in a semi-arid environment, of *Eucalyptus camaldulensis* Dehnh. from two provenances. *Aust. J. Bot.* 29:97–110.
- Morris, J.D. and L.A.J. Thomson. 1983. The role of trees in dryland salinity control. *Proc. R. Soc. Vict.* 95:123–131.
- Nemani, R.R. and S.W. Running. 1989. Testing a theoretical climate-soil-leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agric. For. Meteorol.* 44:245–260.
- Olbrich, B.W. 1991. The verification of the heat pulse technique for estimating sap flow in *Eucalyptus grandis*. *Can. J. For. Res.* 21:836–841.
- Pidsley, D., E. Kerle, D. Williams, T.J. Hatton and B. Myers. 1994. Role of transpiration in the recharge/discharge process of an aquifer system underlying open eucalypt forest in wet/dry North Australian tropics. *Proc. Water Down Under '94*, Adelaide, pp 491–496.
- Pierce, L.L., J. Walker, T.I. Dowling, T. McVicar, T.J. Hatton, S.W. Running and J.C. Coughlan. 1993. Hydroecological changes in the Murray-Darling Basin: Part 3—A simulation of regional hydrological changes. *J. Appl. Ecol.* 30:283–294.
- Pomeroy, L.R., E.C. Hargrove and J.J. Alberts. 1988. The ecosystem perspective, *In* Concepts of Ecosystem Ecology: A Comparative View, Ecological Studies: Analysis and Synthesis, Vol. 67. Eds. L.R. Pomeroy and J.J. Alberts. Springer-Verlag, New York, pp 1–17.
- Pook, E.W. 1986. Canopy dynamics of *Eucalyptus maculata* Hook. IV. Contrasting responses to two severe droughts. *Aust. J. Bot.* 34:1–14.
- Roberts, J. 1983. Forest transpiration: a conservative hydrological process? *J. Hydrol.* 66:133–141.
- Siberstein, R.P. 1996. An investigation of water and energy balances at small catchment scales: modelling and validation. Ph.D. Thesis, University of Western Australia, Nedlands, 220 p.
- Specht, R.L. 1972. Water use by perennial evergreen plant communities in Australia and Papua New Guinea. *Aust. J. Bot.* 20:273–299.
- Specht, R.L. and A. Specht. 1989. Canopy structure in *Eucalyptus*-dominated communities in Australia along climatic gradients. *Acta Oecol. Oecol. Plant.* 10:191–213.
- Swanson, R.H. and D.W.A. Whitfield. 1981. A numerical analysis of heat pulse velocity theory and practice. *J. Exp. Bot.* 32:221–239.
- Szicz, G. and I.F. Long. 1969. Surface resistance of crop canopies. *Water Resour. Res.* 5:622–633.
- Turner, N.C. 1991. Measurement and influence of environmental and plant factors on stomatal conductance in the field. *Agric. For. Meteorol.* 54:137–154.
- Vertessy, R.A., R.G. Benyon, S.K. O'Sullivan and P.R. Gribben. 1994. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiol.* 15:559–567.
- Werk, K.S., R. Oren, E.-D. Schulze, R. Zimmermann and J. Meyer. 1988. Performance of two *Picea abies* (L.) Karst. Stands at different stages of decline. III. Canopy transpiration of green trees. *Oecologia* 76:519–524.