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Effects of soil water availability on water use efficiency of *Eucalyptus cloeziana* and *Eucalyptus argophloia* plants

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Abstract. Effects of soil water availability on transpiration efficiency (WUE_T), instantaneous water use efficiency (WUE_i) and carbon isotope composition ($\delta^{13}C$) were investigated in 7-month-old plants of humid coastal (Gympie) and dry inland (Hungry Hills) provenances of *Eucalyptus cloeziana* F.Muell. and in a dry inland provenance of *E. argophloia* Blakely (Chinchilla), supplied with 100 (W_{100}), 70 (W_{70}) and 50% (W_{50}) of their water requirements. At W_{100}, WUE_T of the three provenances were not significantly different but as available soil moisture decreased, *E. argophloia* produced greater biomass and demonstrated significantly higher WUE_T than either *E. cloeziana* provenance. Midday WUE_i was not significantly affected by watering regime within each provenance but was lowest in *E. argophloia*. A decrease in soil water availability caused a consistent increase in $\delta^{13}C$ values in all three provenances; however, $\delta^{13}C$ values of *E. argophloia* in all three water regimes were significantly lower than those of *E. cloeziana* provenances, which did not differ significantly from each other. For all three provenances, $\delta^{13}C$ was not correlated with WUE_i but height and root collar diameter were negatively correlated to $\delta^{13}C$. There was little evidence of differences in $\delta^{13}C$, WUE_T and WUE_i between *E. cloeziana* provenances but clear differences between *E. cloeziana* and *E. argophloia*. The high WUE_T, low WUE_i and low $\delta^{13}C$ for *E. argophloia* may have implications in the selection of *Eucalyptus* provenances for commercial forestry in low-rainfall regions.

Introduction

Plantation forestry in Queensland, Australia, is currently limited to the coastal south-east region where annual rainfall is greater than 1000 mm. However, owing to limited availability of land for further expansion, there is a need to explore the potential for cultivation of native hardwood species in the low-rainfall zone with annual rainfall between 700 and 1000 mm (Loxton and Forster 2000). Most eucalypt species from lower rainfall areas can tolerate intermittent drought (Boland *et al.* 1984), but the main emphasis in planted forests is on wood production rather than survival, which may be appropriate in a natural growth environment (Olbrich *et al.* 1993). Generally, when water supply is limited, plants that use water more efficiently and have the ability to grow rapidly when soil moisture is not limiting should have greater productivity than plants with low water use efficiency (Jones 1993; Zhang *et al.* 1997). Consequently, knowledge of water use efficiency is required for the selection of species for plantings in low-rainfall regions.

Several measures of water use efficiency include transpiration efficiency (WUE_T), defined as the ratio of biomass produced by a plant to the amount of water lost through transpiration (Calder 1992; Osório and Pereira 1994; Zhang and Marshall 1994; Turner 1997; Li 2000; Li *et al.* 2000); instantaneous water use efficiency (WUE_i), defined as the ratio of net photosynthesis (A) to stomatal conductance (g_s) (A/g_s) (Ni and Pallardy 1991; Ehleringer *et al.* 1993; Osório *et al.* 1998*a*; Pinkard *et al.* 1998); and carbon isotope composition ($\delta^{13}C$) (and carbon isotope discrimination ($\triangle$), the ratio of ^{13}C to ^{12}C in plant material (Farquhar *et al.* 1982; Farquhar and Richards 1984; Osório and Pereira 1994; Osório *et al.* 1998*a*; Xu *et al.* 2000). Both WUE_T and carbon isotope ratios integrate physiological and environmental properties that influence photosynthetic and transpirational gas exchange over the period of growth (Jones 1993; Zhang and Marshall 1994; Turner 1997). In particular, the use of $\delta^{13}C$ may provide a rapid and practical technique for the screening of large numbers of genotypes for water use efficiency (Farquhar and Richards 1984;

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Donovan and Ehleringer 1994), which could be especially useful for early screening of long-lived forestry species (Farquhar and Richards 1984; Bond and Stock 1990; Olbrich *et al.* 1993; Donovan and Ehleringer 1994; Osório *et al.* 1998*b*; Xu *et al.* 2000).

Mäkelä *et al.* (1996) predicted that plants originating from a wet environment would have an aggressive water use behaviour, with low water use efficiency, while plants from a dry environment would have high water use efficiency. Similarly, Li *et al.* (2000) reported that the WUE_T of *E. microtheca* F.Muell. plants increased with increase in drought. However, a comparison between $\delta^{13}C$ of desert shrubs and montane trees by DeLucia and Schlesinger (1991) suggested that drought-tolerant shrubs had lower water use efficiency than montane trees. Jones (1993) has argued that under conditions of limited water, selecting for high water use efficiency may mean selecting for low productivity, because water conserved by such a species in a competitive environment would increase moisture availability for evaporation and for potential competitors (DeLucia and Heckathorn 1989; DeLucia and Schlesinger 1991; Korol *et al.* 1999).

Eucalyptus cloeziana and *E. argophloia* have been identified as two priority species for hardwood forest plantings in the subtropical region of Queensland and New South Wales (Keenan *et al.* 1998). *E. cloeziana* has a wide natural distribution in humid and subhumid eastern Queensland (annual rainfall varies greatly between 550 and 2300 mm), occurring in four disjunct geographical regions: southern coastal, southern inland, northern coastal and northern inland (Turnbull 1979; Boland *et al.* 1984). This suggests that the species may have a high level of genetic variability. Satisfactory growth of planted trees of Gympie (coastal), Hungry Hills and Coominglah (inland) provenances has been obtained on sites having an annual rainfall greater than 1200 mm within Australia, Brazil, Congolese People's Republic, Zambia and Zimbabwe (Lee *et al.* 1997; Eerikainen *et al.* 1999). *E. argophloia* is a potential commercial timber species with a narrow natural distribution north-east of Chinchilla in southern inland Queensland, where it occurs under warm subhumid conditions (700 mm mean annual rainfall) (Boland *et al.* 1984). There is a dearth of knowledge about the water use of these two species.

This study reports an investigation on the relationships between water use efficiency and soil water availability of three provenances of two *Eucalyptus* species: *E. argophloia* and inland (dry) and coastal (humid) provenances of *E. cloeziana*. It was hypothesised that (1) dry inland provenances (*E. argophloia* and a Hungry Hills provenance of *E. cloeziana*) would have a higher water use efficiency under low water conditions than the humid (less drought-tolerant) coastal provenance of *E. cloeziana* from Gympie; and (2) that the amount of biomass produced per unit of water used in transpiration would depend on the amount of available water. Accordingly, the objectives of the investigation were to determine for each of the three provenances whether (1) transpiration efficiency, instantaneous water use efficiency and carbon isotope composition vary among the three provenances; (2) a decrease in soil moisture availability would lead to higher water use efficiency and (3) $\delta^{13}C$ was related to measures of water use efficiency (WUE_T and WUE_i).

Materials and methods

Seedling and growth conditions

Seedlings of *E. argophloia* and a dry and a humid provenance of *E. cloeziana* (seed collection details given in Table 1) were raised in pots containing a 50:50 mixture of peat and vermiculite at the Queensland Forestry Research Institute (QFRI), Gympie. In June 2000, the 6-month-old seedlings were moved to the University of Queensland glasshouse facility (Brisbane) and transferred into plastic pots (175 mm diameter × 175 mm deep) lined with polythene and containing nursery top soil (loam-textured) mixed with vermiculite and perlite in the ratio of 4:1:1. Slow-release fertiliser (Omocote Plus (3–4 months) containing micronutrients) was mixed with the potting medium at a rate of 2 kg m^{-3}. The pots were maintained in a naturally illuminated glasshouse with temperature control provided by evaporative coolers and electric fan heaters. Over the 96-day experimental period (August–November 2000), daytime temperatures in the glasshouse ranged from 21 to 37°C.

Watering regimes

Sixty healthy seedlings of uniform height were chosen from each provenance, and white plastic beads were spread on the soil surface of each pot to minimise evaporation (Myers and Landsberg 1989). The experiment comprised three provenances and three watering regimes (field capacity, 70 and 50% of field capacity) with 20 seedlings per treatment combination. The pots were arranged in a completely randomised design on benches which were rotated every 2 days to

Table 1. Seedlot information on the three *Eucalyptus* taxa used in the experiments (seed provided by The Queensland Department of Primary Industries—Forestry)

Provenance	Seedlot number	No. of parent trees	Locality	Origin Latitude, longitude	Altitude (m)	Mean annual rainfall (mm)
E. cloeziana (humid)	4363	11	SF 949 Goomboorian (Downsfield LA)	26°03′S, 152°42′E	110	1210
E. cloeziana (dry)	10823	20	SF 57 Mungy (Hungry Hills)	25°18′S, 151°22′E	310	780
E. argophloia	5520	18	SF 302 Ballon	26°20′S, 150°20′E	300	650

minimise the effect of environmental heterogeneity, and the seedlings were well spaced to avoid shading one another.

A 2-day watering schedule was applied throughout the experiment. Plants in the control treatment (100% of field capacity, W_{100}) were rewatered every 2 days with an amount of water equivalent to that lost through evapotranspiration. The loss was estimated by determining the mean weight change of five pots of the W_{100} regime of each provenance. Water-stressed plants received 70 (W_{70}) and 50% (W_{50}) of water supplied to control plants according to the methods of Myers and Landsberg (1989) and Nativ *et al.* (1999). Evaporative water loss from the soil surface was estimated from five pots having white plastic beads spread on the surface and watered to field capacity every 2 days and having a dead *Eucalyptus* twig inserted at the centre (Li *et al.* 2000). Every 2 weeks, the mean fresh weight of three plants from each treatment was used to adjust for pot weight changes resulting from plant growth, while the weights of pots in the W_{70} and W_{50} regimes were adjusted by watering to return soil water levels to 70 and 50% of field capacity (Osório *et al.* 1998*b*). The experiment ran for 96 days.

Transpiration efficiency

Plant biomass was determined at the beginning of the experiment by harvesting five plants from each entity and 96 days later at the end of the experiment by harvesting the five plants from each treatment. Plant components (leaves, stem and roots) were oven-dried to constant weight at 80°C. Transpiration efficiency (WUE_T) (Osório and Pereira 1994; Zhang and Marshall 1994; Turner 1997) was determined by dividing total dry matter production of each plant by the total amount of water transpired throughout the growing period. Stem water use efficiency (WUE_s) (Le Roux *et al.* 1996) was determined by dividing total dry matter of the stem of each plant by the total amount of water transpired by the plant throughout the growing period.

Gas exchange

Gas exchange was measured at ambient CO_2 concentration (350–370 $\mu mol\ m^{-2}\ s^{-1}$) in the glasshouse. Measurements were taken at about midday by using a portable photosynthesis system (model LI-6200, Li-Cor Inc., Lincoln, NE, USA) equipped with a 250-mL cuvette. Gas exchange was measured on a young, fully expanded leaf under bright sunlight when photosynthetic photon flux density (PPFD) was greater than 700 $\mu mol\ m^{-2}\ s^{-1}$. Since leaf-to-air vapour pressure deficit did not vary substantially during midday (Donovan and Ehleringer 1994), the instantaneous water use efficiency (WUE_i) was determined by dividing net photosynthetic rate (A) by stomatal conductance (g_s) (Ehleringer *et al.* 1993; Osório *et al.* 1998*a*; Pinkard *et al.* 1998).

Carbon isotope composition

More than 95% of the leaves present at the end of the experiment had formed during the experiment. All leaves of each plant were oven-dried and finely ground by using a ball mill. Subsamples were taken for the determination of relative abundance of ^{13}C and ^{12}C by using the isotope ratio mass spectrometer facilities at the University of Queensland and Griffith University, Brisbane. The $^{13}C/^{12}C$ ratios were calculated against PeeDee Belemnite standard (^{13}C) and the precision of the analyses was ± $0.3^{o}/_{oo}$. Carbon isotope composition ($\delta^{13}C$) was used rather than discrimination ($\triangle$) because $\delta^{13}C$ of the air was not measured and CO_2 recycling could have occurred in the glasshouse, thus altering the $\delta^{13}C$ of the air (Osório and Pereira 1994).

Data analysis

Two- and one-way analyses of variance were used to determine the effects of water availability and provenances on WUET, WUEi and δ13C. Relationships between variables were analysed by linear regression methods and Pearson's correlation coefficients (SAS Institute Inc. 1985). Means were compared by Duncan's multiple range test (SAS Institute Inc. 1985). Differences were considered significant at $P \leq 0.05$.

Results

Over the 96-day test period, water consumption of the humid provenance of *E. cloeziana* was reduced by 59% in the W_{70} regime and 75% in the W_{50} regime, and for the dry provenance by 56% in the W_{70} regime and 84% in the W_{50} regime relative to the W_{100} regime. In *E. argophloia*, water consumption was reduced by 40% in the W_{70} regime and by 62% in the W_{50} regime relative to the control regime (W_{100}) (Table 2). Water consumption was reduced more in the *E. cloeziana* provenances than in *E. argophloia*. Reduced biomass production in the W_{50} and W_{70} regimes of *E. cloeziana* corresponded with the decrease in water consumption, while in *E. argophloia* dry matter production was relatively less affected by decreased soil moisture availability.

Total biomass production and total water consumption were both positively correlated with total leaf area production per plant in all three provenances (Fig. 1).

Table 2. Effects of three watering regimes on total dry matter production, quantity of water lost through transpiration, water use efficiency and carbon isotope composition of *Eucalyptus cloeziana* and *E. argophloia*

Water regimes were 100 (W_{100}), 70 (W_{70}) and 50% (W_{50}) of field capacity. Each value is the mean of five plants ± standard error of mean. Within each provenance and for each attribute, means with the same letter (a–c) were not significantly different ($P = 0.05$). Among provenances, water regime and for each attribute, means followed by the same letter (x–z) were not significantly different ($P = 0.05$); DM, dry matter; WUE_T, water use efficiency; $\delta^{13}C$, carbon isotope composition

Provenance	Water regime	Total DM (g)	Water loss (kg)	WUE_T (g DM kg^{-1} H_2O)	$\delta^{13}C$ ($^{o}/_{oo}$)
E. cloeziana (humid)	W_{100}	27.80 ± 2.36ay	6.23 ± 0.30ay	4.44 ± 0.20x	–23.88 ± 0.27y
	W_{70}	10.64 ± 1.40by	2.55 ± 0.02bz	4.16 ± 0.51y	–23.70 ± 0.30y
	W_{50}	7.01 ± 0.66by	1.56 ± 0.01cy	4.49 ± 0.42y	–23.32 ± 0.28y
E. cloeziana (dry)	W_{100}	28.80 ± 1.70ay	6.31 ± 1.02ay	4.73 ± 0.58x	–24.16 ± 0.30y
	W_{70}	13.42 ± 1.12by	2.78 ± 0.02by	4.81 ± 0.38xy	–23.58 ± 0.28y
	W_{50}	5.01 ± 0.33cy	1.03 ± 0.02cz	4.90 ± 0.36y	–23.07 ± 0.33y
E. argophloia	W_{100}	58.03 ± 1.55ax	10.82 ± 0.42ax	5.38 ± 0.14x	–26.43 ± 0.33bx
	W_{70}	38.33 ± 2.30bx	6.51 ± 0.08bx	5.88 ± 0.31x	–25.77 ± 0.28abx
	W_{50}	25.64 ± 1.92cx	4.08 ± 0.01cx	6.29 ± 0.47x	–25.24 ± 0.30ax

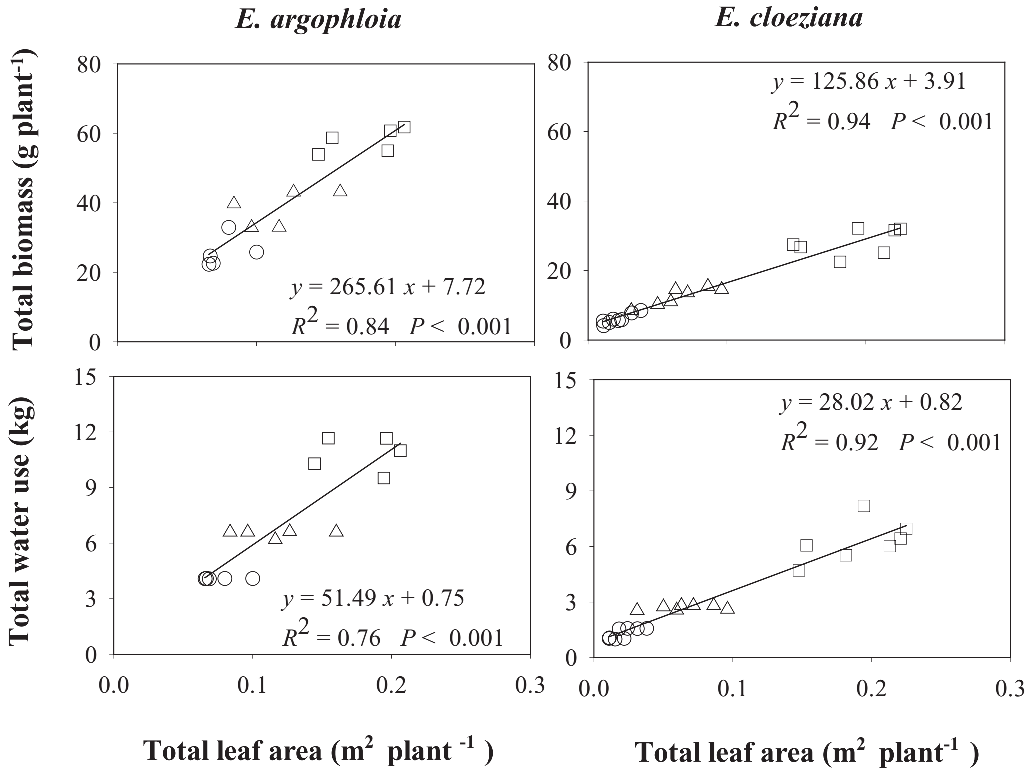

Fig. 1. Relationships between total leaf area production per plant, total water use and biomass production of *Eucalyptus argophloia* and *E. cloeziana* provenances grown under three watering regimes. □, W_{100}; △, W_{70}; ○, W_{50}).

Although the biomass produced per unit leaf area in *E. cloeziana* was half that produced by *E. argophloia*, *E. argophloia* used twice as much water per unit of leaf area (Table 2). There were large differences in the amount of water used between treatments within a provenance, but WUE_T values within each provenance did not differ significantly ($P > 0.05$, Table 2), indicating that biomass production was proportional to the available water. Under W_{100} regimes, the WUE_T values of the three provenances were significantly ($P = 0.08$) different, whereas at W_{70}, the WUE_T of *E. argophloia* (5.88 ± 0.31 g DM kg^{-1} H_2O) and that of the dry provenance (4.81 ± 0.38 g DM kg^{-1} H_2O) of *E. cloeziana* were not significantly different, but the WUE_T of *E. argophloia* was significantly higher than that of the humid provenance (4.16 ± 0.51 g DM kg^{-1} H_2O) (Table 2). In the W_{50} regime, *E. argophloia* (6.29 ± 0.47 g DM kg^{-1} H_2O) demonstrated a significantly higher WUE_T than either of the *E. cloeziana* provenances (Table 2).

There were no significant differences in carbon isotope composition among watering regimes in either of the *E. cloeziana* provenances (Table 2). However, the $\delta^{13}C$ composition of *E. argophloia* plants in the W_{50} regime was significantly greater than in the control regime. The $\delta^{13}C$ values of *E. argophloia* in all three water regimes were significantly smaller than those of *E. cloeziana* provenances, which did not differ significantly from each other (Table 2).

Within each provenance, net photosynthesis, stomatal conductance and transpiration rates were significantly higher in the W_{100} treatments than in the W_{70} and W_{50} treatments, which did not differ from each other (Table 3). In all three water treatments, the rates of transpiration for *E. argophloia* were 63% higher than those of the humid and dry provenances of *E. cloeziana* (Table 3). Although both A and g_s decreased in plants subjected to soil water deficit, they were higher in *E. argophloia* than in *E. cloeziana* provenances. Midday WUE_i was not significantly affected by watering regime within each provenance (Table 3). However, in the W_{100} regime, WUE_i of *E. argophloia* was significantly lower than that of the *E. cloeziana* provenances, which did not differ significantly (Table 3). No significant differences in WUE_i among provenances were observed at W_{70} and W_{50}. The WUE_i of *E. argophloia* on each measurement occasion was consistently lower than that of *E. cloeziana* provenances, but for all three provenances it decreased with increase in plant age (Table 3).

There were positive but weak correlations between WUE_T and ^{13}C in the humid and dry provenances of *E. cloeziana* but a strong positive correlation was observed in *E. argophloia*

Table 3. Effects of three watering regimes on net photosynthetic rate, stomatal conductance (g_s) the rate of transpiration and instantaneous water use efficiency of the humid and dry provenances of *Eucalyptus cloeziana* and *E. argophloia*

Water regimes were 100 (W_{100}), 70 (W_{70}) and 50% (W_{50}) of field capacity. Each value is the mean of five plants ± standard error of mean. Within each provenance and for each attribute, means with the same letter (a–c) were not significantly different ($P = 0.05$). Among provenances, water regime and for each attribute, means followed by the same letter (x–z) were not significantly different ($P = 0.05$). A, net photosynthetic rate; g_s, stomatal conductance; E, rate of transpiration; $\mathrm{WUE_i}$, instantaneous water use efficiency

Provenance	Water regime	A (μmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	$\mathrm{WUE_i}$ (A/g_s) (μmol mmol^{-1})
E. cloeziana (humid)	W_{100}	7.83 ± 0.81ay	70.50 ± 9.77ay	2.25 ± 0.20ay	0.121 ± 0.007x
	W_{70}	4.09 ± 1.21by	36.98 ± 5.04by	1.63 ± 0.17aby	0.114 ± 0.012x
	W_{50}	2.86 ± 1.03ay	36.21 ± 4.23by	1.43 ± 0.23by	0.098 ± 0.012x
E. cloeziana (dry)	W_{100}	8.06 ± 0.41ay	67.25 ± 9.06ay	2.63 ± 0.17ay	0.126 ± 0.008x
	W_{70}	4.15 ± 1.22by	38.54 ± 8.36by	1.97 ± 0.09by	0.121 ± 0.016x
	W_{50}	2.34 ± 1.67by	23.34 ± 7.22bz	1.44 ± 0.30by	0.109 ± 0.020x
E. argophloia	W_{100}	13.45 ± 0.59ax	194.26 ± 16.03ax	6.69 ± 0.57ax	0.076 ± 0.006y
	W_{70}	9.47 ± 0.93bx	148.01 ± 19.01abx	4.90 ± 0.67abx	0.078 ± 0.013x
	W_{50}	8.67 ± 1.03bx	106.15 ± 15.9bx	3.85 ± 0.19bx	0.086 ± 0.010x

Table 4. Pearson's correlation coefficients and probability levels between transpiration efficiency, stem water use efficiency (ratio of stem dry weight to water used in evapotranspiration), root collar diameter and plant height and carbon isotope composition obtained from pooled data for each provenance of *Eucalyptus* species

r, Pearson's correlation coefficients; P probability levels; $\mathrm{WUE_T}$, transpiration efficiency; $\mathrm{WUE_s}$, stem water use efficiency; δ^{13}C, carbon isotope composition

Dependent variable	Independent variable	Parameter	*E. cloeziana* dry	*E. cloeziana* humid	*E. argophloia*
$\mathrm{WUE_T}$	δ^{13}C	r	0.31	0.01	0.60
		P	<0.41	<0.98	<0.09
$\mathrm{WUE_s}$	δ^{13}C	r	0.86	0.72	0.33
		P	<0.003	<0.04	<0.39
Root collar diameter	δ^{13}C	r	–0.55	–0.35	–0.74
		P	<0.13	<0.39	<0.02
Plant height	δ^{13}C	r	–0.36	0.32	–0.24
		P	<0.34	<0.45	<0.53

(Table 4). For each provenance δ^{13}C was not correlated to $\mathrm{WUE_i}$. There was a weak positive correlation between stem water use efficiency (ratio of stem dry matter to water used in evapotranspiration, $\mathrm{WUE_s}$) and δ^{13}C in *E. argophloia* but a strong positive correlation for the humid and dry provenances of *E. cloeziana* (Table 4). In *E. argophloia* and the dry provenance of *E. cloeziana*, height was negatively and weakly correlated to δ^{13}C, whereas root collar diameter in the three provenances was negatively correlated to δ^{13}C (Table 4).

Discussion

Differences in $\mathrm{WUE_i}$, $\mathrm{WUE_T}$ and δ^{13}C among provenances were identified, indicating differences in plant performance under water deficits. The two inland provenances, *E. argophloia* and the dry provenance of *E. cloeziana*, were hypothesised to exhibit higher water use efficiency under water deficit treatments than the humid coastal provenance of *E. cloeziana*. Only the $\mathrm{WUE_T}$ results for *E. argophloia* supported this hypothesis, while the δ^{13}C results of *E. argophloia* and the dry provenance of *E. cloeziana* showed the contrary relationships. Water use parameters for *E. cloeziana* provenances did not support the hypothesis that water use efficiency increased with decrease in soil moisture availability but the δ^{13}C values for *E. argophloia* showed significantly greater water use efficiency under water deficit conditions. Conversely, there were no significant differences in $\mathrm{WUE_T}$ among watering regimes within each entity (Table 2). There was little evidence of genetic differences in δ^{13}C, $\mathrm{WUE_T}$ and $\mathrm{WUE_i}$ between *E. cloeziana* provenances in the W_{100}, W_{70} and W_{50} watering regimes, but clear evidence of genetic differences between *E. cloeziana* and *E. argophloia*, as reflected by the large differences in absolute values of the three measures of water use efficiency (Tables 2 and 3).

Drought-induced reduction in water consumption was larger in *E. cloeziana* provenances than in *E. argophloia* and corresponded with a decrease in biomass production.

E. argophloia used the most water and produced the greatest biomass under conditions of low water availability, resulting in increased WUE_T. Under all three water regimes, *E. cloeziana* provenances had lower WUE_T than *E. argophloia*. Conversely, $\delta^{13}C$ values showed that *E. cloeziana* provenances had significantly ($P < 0.05$) higher water use efficiency (less negative values) than *E. argophloia* (Table 2). Similarly, the WUE_i values for *E. argophloia* were consistently smaller than those of *E. cloeziana* in all watering regimes (Table 3), implying that the provenance had lower water use efficiency than *E. cloeziana*.

When water was not limiting and all three provenances had similar WUE_T, the biomass production in *E. argophloia* was about twice, whereas WUE_i was about half, that of the *E. cloeziana*. This was associated with higher rates of net photosynthesis, stomatal conductance and transpiration for *E. argophloia* (Table 3). A decrease in water availability in all three provenances was accompanied by a decrease in biomass and a consistent decrease in $\delta^{13}C$ values, although the decrease was only statistically significant for *E. argophloia*. This change in $\delta^{13}C$ during water stress can be related to an increase in hydraulic resistance, an increase in soil resistance or a decrease in leaf conductance (Nilsen and Orcutt 1996).

The greater biomass produced by *E. argophloia* when water supply was limited is related to the ability of the species to maintain greater leaf area (Fig. 1) and higher rates of photosynthesis (Table 3), and implies that the species is able to use limited water supplies more efficiently and hence has a greater ability to grow under such conditions (Zhang *et al.* 1997) than *E. cloeziana* plants. The low WUE_T of *E. cloeziana* is consistent with that reported for wet climate populations of *E. microtheca* and is consistent with the notion of optimal plant functioning being represented by a pattern of more aggressive water use in plants from wet climates than those from dry areas (Mäkelä *et al.* 1996). Consequently, the high values of $\delta^{13}C$ obtained for *E. cloeziana* (>–24.16) may be subject to misinterpretation when being compared with those for *E. argophloia* (<–25.24). This pattern may reflect either differences in WUE or systematic differences in plant fractionation of reduced carbon into lipids, lignin, protein and cellulose which have different $\delta^{13}C$ values (Nilsen and Orcutt 1996). Another factor contributing to the greater $\delta^{13}C$ value in *E. cloeziana* relative to *E. argophloia* may have been the rapid decrease of midday stomatal conductance in proportion to photosynthesis (Cowan 1982; Osório and Pereira 1994), relative to those of *E. argophloia* plants, as has been reported for *Pinus ponderosa* Laws. (montane tree) and *Artemisia tridentata* Nutt. (desert shrub) (DeLucia and Heckathorn 1989).

The correlation between WUE_T and $\delta^{13}C$ in this study was very poor (Table 4), unlike the strong positive correlation reported for *E. globulus* Labill. clones (Osório and Pereira 1994; Osório *et al.* 1998*a*), for western larch (*Larix occidentalis* Nutt.) (Zhang and Marshall 1994) and for *E. microtheca* (Li 2000). This was unexpected because the two variables WUE_T and $\delta^{13}C$ are related through their independent links to the ratio of intercellular to atmospheric CO_2 concentration (C_i/C_a) (Farquhar and Richards 1984). However, Le Roux *et al.* (1996) also found no significant correlation between the two variables in 16-month-old clones of *E. grandis* (Hill ex Maiden). In this study, it is likely that this relationship was complicated by differences in carbon allocation, internal gas exchange characteristics and environmental factors such as average vapour pressure difference and water availability, or their interaction (Farquhar *et al.* 1982; Olbrich *et al.* 1993; Osório *et al.* 1998*a*; Li 2000). Similarly, since both $\delta^{13}C$ and WUE_i are independently related to C_i/C_a, a positive association is expected between them (Farquhar *et al.* 1982). A positive correlation was reported for *E. globulus* clones when WUE_i data were measured in late morning hours, during the time that maximum daily leaf conductance occurred (Osório *et al.* 1998*a*). The midday gas exchange data set used in this study did not indicate a significant correlation between WUE_i and $\delta^{13}C$, consistent with the results reported for *E. grandis*, *E. grandis* × *camaldulensis* and *E. grandis* × *nitens* clones in a field site (Le Roux *et al.* 1996). Similarly, rising temperature, vapour pressure deficit and high photon flux density in the glasshouse at midday may have inhibited rates of gas exchange relative to mid-morning rates, thereby affecting WUE_i values.

Although an increase in plant height as $\delta^{13}C$ value becomes more positive has been reported for western larch families (Zhang *et al.* 1996), for F_1 hybrids between slash pine and Caribbean pine (Xu *et al.* 2000) and for 8-year-old *Araucaria cunninghamii* Ait. ex D. Don. families (Prasolova *et al.* 2000), an increase in tree height as $\delta^{13}C$ value becomes more negative has also been reported in 13-month-old clones of *Eucalyptus grandis* (Bond and Stock 1990), suggesting that trees less efficient at water use were more productive. Le Roux *et al.* (1996) found no correlation between the water use of harvestable stem and $\delta^{13}C$ of *E. grandis* hybrids. In this study, both height and root collar diameter were negatively correlated to $\delta^{13}C$ and when water use was calculated as the ratio of shoot biomass (excluding leaf biomass) to the amount of water transpired, there was a strong positive correlation for both *E. cloeziana* provenances but a poor correlation for *E. argophloia*.

Eucalyptus argophloia exhibited greater drought tolerance than *E. cloeziana*, as shown by higher net photosynthetic rates and greater biomass production under conditions of water deficit (Table 3). However, *E. cloeziana* had higher $\delta^{13}C$ values than *E. argophloia*, implying greater water use efficiency. In irrigated and fertilised *E. grandis* grown in different climates in Australia, trees grown at a wet site at Gympie had a higher $\delta^{13}C$ value than trees growing at sites with higher vapour pressure deficit (Korol *et al.* 2000). Similarly, the increase in water use efficiency as water deficit stress increased in this study was attributed to the greater decrease in stomatal conductance in *E. cloeziana* than in *E. argophloia*. The low water use efficiency of *E. argophloia*, indicated by relatively smaller $\delta^{13}C$ values in this study, was consistent with that reported for Great Basin desert shrubs compared with Sierran montane tree species (DeLucia and Schlesinger 1991) and supports the contention that in a competitive environment there is likely to be no advantage from a reduction in water use by an individual plant if that water becomes available to neighbouring plants (Jones 1993; Hunt *et al.* 1999; Korol *et al.* 1999).

The combination of attributes for *E. argophloia* in this study supports the suggestion of DeLucia and Heckathorn (1989) that the combination of low water use efficiency ('profligate' use of water) and high degree of drought tolerance as exemplified by *Artemisia tridentata* when compared with *Pinus ponderosa*, may be a more ecologically successful combination of physiological characteristics in most water-limited habitats. Moreover, Donovan and Ehleringer (1994) have also suggested that low water use efficiency may be advantageous for young or small establishing plants if it is associated with greater biomass accumulation. This study demonstrates the complexity of using different water use efficiency indices in the selection of planting material for low rainfall environments. Relatively high biomass production in *E. argophloia* was associated with high WUE_T values and low water use efficiency implied by low $\delta^{13}C$ and WUE_i values, while small biomass production in *E. cloeziana* was associated with low WUE_T and high $\delta^{13}C$ and WUE_i. These results imply that *E. argophloia* has the potential for wood production in both the subhumid and humid environments, whereas the dry and the humid provenances of *E. cloeziana* have higher wood production potential on humid than on subhumid environments.

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References

Boland DJ, Brooker MIH, Chippendale GM, Hall N, Hyland BPM, Johnson RD, Kleinig DA, Turner JD (1984) 'Forest trees of Australia.' (Thomas Nelson Australia and CSIRO: Melbourne)

Bond WJ, Stock WD (1990) Preliminary assessment of the grading of *Eucalyptus* clones using carbon isotope discrimination. *South African Journal of Forestry* **154**, 51–55.

Calder IR (1992) Water use of eucalyptus. In 'Growth and water use of forest plantations'. (Eds IR Calder, RL Hall, PG Adlard) pp. 167–179. (Wiley: Chichester, England)

Cowan IR (1982) Regulation of water use in relation to carbon gain in higher plants. *Encyclopedia of Plant Physiology* **12B**, 489–613.

DeLucia EH, Heckathorn SA (1989) The effect of soil drought on water-use efficiency in a contrasting Great Basin desert and Sierran montane species. *Plant, Cell and Environment* **12**, 935–940.

DeLucia EH, Schlesinger WH (1991) Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology Journal* **72**, 51–58.

Donovan LA, Ehleringer JR (1994) Potential for selection on plants for water-use efficiency as estimated by carbon isotope discrimination. *American Journal of Botany* **81**, 927–935.

Eerikainen KPA, Mabvurira D, Saramaki J (1999) Alternative taper curve estimation methods for *Eucalyptus cloeziana* F.Muell. *Southern African Journal of Forestry* **184**, 12–24.

Ehleringer JR, Hall AE, Farquhar GD (1993) 'Stable isotopes and plant carbon-water relations.' (Academic Press: San Diego; Sydney)

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration. *Australia Journal of Plant Physiology* **9**, 121–137.

Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* **11**, 539–552.

Hunt MA, Unwin GL, Beadle C (1999) Effect of naturally regenerated *Acacia dealbata* on the productivity of a *Eucalyptus nitens* plantation in Tasmania, Australia. *Forest Ecology and Management* **117**, 75–85.

Jones HG (1993) Drought tolerance and water use efficiency. In 'Water deficits: plant responses from cell to community'. (Eds JAC Smith, H Griffiths) pp. 193–203. (BIOS Scientific Publishers Ltd: Oxford)

Keenan RJ, Ivory M, Lawson S, Lee D, Leggate W, Lewty MJ, Nikles DG, Ryan P, Walker S (1998) Hardwood plantation research and development: a strategy to support a hardwood plantation industry in Queensland. Queensland Forestry Research Institute, Report, Brisbane.

Korol RL, Kirschbaum MUF, Farquhar GD, Jeffreys M (1999) Effects of water status and soil fertility on the C-isotope signature in *Pinus radiata*. *Tree Physiology* **19**, 551–562.

Korol RL, Kirschbaum MUF, Myers JB (2000) Carbon Isotope Discrimination of irrigated and fertilized *Eucalyptus grandis* grown in different climate. CSIRO Forest and Forest Products, Report no. 120, Kingston, ACT.

Le Roux D, Stock WD, Maphanga D (1996) Dry mass allocation, water use efficiency and delta ^{13}C in clones of *Eucalyptus grandis*, *E. grandis* × *camaldulensis* and *E.gradis* × *nitens* grown under two irrigation regimes. *Tree Physiology* **16**, 497–502.

Lee D, Ryan P, Nikles G. (1997). Provenance variation of *Eucalyptus cloeziana* exhibited at Pomona in South eastern Queensland. In 'Overcoming impediments to reforestation: tropical forest rehabilitation in the Asia-Pacific region', Proceedings of the 6th international workshop of biotechnology assisted reforestation (Bio-Refor). Brisbane, Australia. (Eds J Kikkawa, P Dart, D Doley, K Ishii, D Lamb, K Suzuki) pp. 187–189. (BIO-REFOR)

Li C (2000) Population differences in water-use efficiency of *Eucalyptus microtheca* seedlings under different watering regimes. *Physiologia Plantarum* **108**, 134–139.

Li C, Berninger F, Koskela J, Sonninen E (2000) Drought responses of *Eucalyptus microtheca* provenances depend on seasonality of rainfall in their place of origin. *Australian Journal of Plant Physiology* **27**, 231–238.

Loxton I, Forster S (2000) Brigalow research station technical report 1999–2000. Queensland Beef Industry Institute, Department of Primary Industries, Queensland, Report no. Q100098, Theodore.

Mäkelä A, Berninger F, Hari P (1996) Optimal control of gas exchange during drought: theoretical analysis. *Annals of Botany* **77**, 461–467.

Myers BJ, Landsberg JJ (1989) Water stress and seedling growth of two eucalypt species from contrasting habitats. *Tree Physiology* **5**, 207–218.

Nativ R, Ephrath JE, Berliner PR, Saranga Y (1999) Drought resistance and water use efficiency in *Acacia saligna. Australian Journal of Botany* **47**, 577–586.

Ni B-R, Pallardy SG (1991) Response of gas exchange to water stress in seedlings of woody angiosperms. *Tree Physiology* **8**, 1–9.

Nilsen ET, Orcutt DM (1996) 'The physiology of plants under stress: abiotic factors.' (Wiley: New York)

Olbrich BW, Le Roux D, Poulter AG, Bond WJ, Stock WD (1993) Variation in water use efficiency and $\delta^{13}C$ levels in *Eucalyptus grandis* clones. *Journal of Hydrology* **150**, 615–633.

Osório J, Osório ML, Chaves MM, Pereira JS (1998*a*) Effects of water deficits in ^{13}C discrimination and transpiration efficiency of *Eucalyptus globulus* clones. *Australian Journal of Plant Physiology* **25**, 645–653.

Osório J, Osório ML, Chaves MM, Pereira JS (1998*b*) Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. *Tree Physiology* **18**, 363–373.

Osório J, Pereira JS (1994) Genotypic differences in water use efficiency and ^{13}C discrimination in *Eucalyptus globulus*. *Tree Physiology* **14**, 871–882.

Pinkard EA, Beadle CL, Davidson NJ, Battaglia M (1998) Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. *Trees* **12**, 119–129.

Prasolova NV, Xu ZH, Farquhar GD, Saffigna PG, and Dieters MJ (2000) Variation in branchlet $\delta^{13}C$ in relation to branchlet nitrogen concentration and growth in 8-year-old hoop pine families (*Araucaria cunninghamii*) in subtropical Australia. *Tree Physiology* **20**, 1049–1055.

SAS Institute Inc. (1985) 'SAS/STAT^{TM} guide for personal computers.' (SAS Institute Inc.: Cary, NC)

Turnbull JW (1979) Geographic variations in *Eucalyptus cloeziana*. PhD Thesis, Australian National University.

Turner NC (1997) Further progress in crop water relations. *Advances in Agronomy* **58**, 293–325.

Xu ZH, Saffigna PG, Farquhar GD, Simpson JA, Haines RJ, Walker S, Osborne DO, Guinto D (2000) Carbon isotope discrimination and oxygen isotope composition in clones of the F1 hybrid between slash pine and Caribbean pine in relation to tree growth, water-use efficiency and foliar nutrient concentration. *Tree Physiology* **20**, 1209–1217.

Zhang J, Marshall JD (1994) Population differences in water-use efficiency of well-watered and water-stressed western larch seedlings. *Canadian Journal of Forest Research* **24**, 92–99.

Zhang J, Marshall JD, Fins L (1996) Correlated population differences in dry matter accumulation, allocation, and water-use efficiency in three sympatric conifer species. *Forest Science* **42**, 242–249.

Zhang JW, Feng Z, Cregg BM, Schumann CM (1997) Carbon isotopic composition, gas exchange, and growth of three populations of ponderosa pine differing in drought tolerance. *Tree Physiology* **17**, 461–466.

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