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Photosynthetic light and temperature responses of *Eucalyptus cloeziana* and *Eucalyptus argophloia*

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Abstract. Acclimation of gas exchange to temperature and light was determined in 18-month-old plants of humid coastal (Gympie) and dry inland (Hungry Hills) provenances of *Eucalyptus cloeziana* F.Muell., and in those of a dry inland provenance of *Eucalyptus argophloia* Blakely. Plants were acclimated at day/night temperatures of 18/13, 23/18, 28/23 and 33/28°C in controlled-temperature glasshouses for 4 months. Light and temperature response curves were measured at the beginning and end of the acclimation period. There were no significant differences in the shape and quantum-yield parameters among provenances at 23, 28 and 33°C day temperatures. Quantum yield [μmol CO_2 μmol^{-1} photosynthetic photon flux density (PPFD)] ranged from 0.04 to 0.06 and the light response shape parameter ranged from 0.53 to 0.78. Similarly, no consistent trends in the rate of dark respiration for plants of each provenance were identified at the four growth temperatures. Average values of dark respiration for the plants of the three provenances ranged from 0.61 to 1.86 $\mu mol\ m^{-2}\ s^{-1}$. The optimum temperatures for net photosynthesis increased from 23 to 32°C for the humid- and from 25 to 33°C for the dry-provenance *E. cloeziana* and from 21 to 33°C for *E. argophloia* as daytime temperature of the growth environment increased from 18 to 33°C. These results have implications in predicting survival and productivity of *E. cloeziana* and *E. argophloia* in areas outside their natural distribution.

Introduction

The forest industry in Queensland, Australia, is committed to the expansion of its plantation resource with some 300 000 ha of new plantations to be established by the year 2020 (The 2020 Vision 1997). The current planted forests in Queensland are concentrated in the humid coastal region with mean annual rainfall greater than 1000 mm. However, with high prices and low availability of land suitable for commercial forestry in this zone, further expansion will only occur on low-rainfall areas (600–1000 mm) (Keenan *et al.* 1998; Loxton and Forster 2000) characterised by large diurnal and seasonal fluctuations in temperature in the range of –10 to 45°C (Bureau of Meteorology 2002). *Eucalyptus cloeziana* and *E. argophloia* are among the priority native species for forest plantation establishment in subtropical and tropical Queensland (Keenan *et al.* 1998). Because little is known of the environmental tolerances of these species, an understanding of the effects of changes in temperature and light on physiological processes is needed for matching these species with available sites.

The ability to tolerate seasonal and diurnal fluctuations in temperature within a single genotype indicates phenotypic plasticity (acclimation) (Weis and Berry 1988; Nilsen and Orcutt 1996). Photosynthesis is temperature-dependent and has an optimum temperature at which the net rate of CO_2 fixation is maximal (Säll and Pettersson 1994). Plants growing in different environments have different optima for photosynthesis, with plants in colder environments having lower temperature optima than those in warmer climates (Slatyer and Ferrar 1977*b*; Björkman *et al.* 1980; Xiong *et al.* 1999). Short-term changes in ambient temperature cause photosynthetic activity to alter, followed by a rapid return to its previous condition when optimum temperature is restored (Säll and Pettersson 1994; Battaglia *et al.* 1996). This observed shift in temperature optimum for net photosynthesis and modification of the peak photosynthetic rate at the optimum temperature with changing growth temperature may change over the course of hours to weeks (Ferrar *et al.* 1989; Säll and Pettersson 1994; Teskey and Will 1999). It is generally argued that this phenomenon is likely

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

MAT, mean of mean monthly minimum and maximum temperatures; MinMin, mean minimum temperature of the coldest month; MaxMax, mean maximum temperature of the hottest month; Alt, altitude; MAR, mean annual rainfall

Provenance	Seedlot number	Origin				Temperature (°C)		
		Locality	Latitude, longitude	Alt. (m)	MAR (mm)	MAT	MinMin	MaxMax
E. cloeziana humid	4363	SF 949 Goomboorian (Downsfield LA)	26°03′S, 152°42′E	110	1210	19.2	5.3	30.6
E. cloeziana dry	10823	SF 57 Mungy (Hungry Hills)	25°18′S, 151°22′E	310	780	19.9	7.2	30.0
E. argophloia	5520	SF 302 Ballon	26°20′S, 150°20′E	300	650	18.9	3.7	32.0

to be most evident in woody species (Nilsen and Orcutt 1996), and particularly in those that are found over a wide range of growing conditions (Read 1990) and are subjected to large seasonal variations in temperature (Björkman *et al.* 1980). Detailed studies reported for *E. pauciflora* Sieb. ex Spreng (Slatyer 1977*a*), *E. globulus* Labill. and *E. nitens* (Deane & Maiden) Maiden (Battaglia *et al.* 1996) and for several *Eucalyptus* species (Ferrar *et al.* 1989) indicate that differences do occur among eucalypt genotypes in the potential for acclimation, as has been reported for other species such as *Nothofagus* (Read 1990,) and *Pinus taeda* L. (Teskey and Will 1999).

Most studies on temperature response of photosynthetic CO_2 reduction by woody plants have considered the rate of photosynthesis at light saturation (Slatyer 1977*b*; Read 1990; Teskey and Will 1999). However, since leaves in the natural environment experience continually changing temperature and incident PPFD, it is important to consider the interaction between these two (Baker *et al.* 1988). Leverenz and Öquist (1987) described potential productivity at a site as a function of incident photon flux density and the quantum yield of photosynthesis. In C_3 plants, quantum yield has been suggested to increase with decreasing temperature, indicating a tendency for higher potential productivity in cool coastal climates than in warmer continental climates (Leverenz and Öquist 1987). There are no estimates of measures of quantum yield for *E. cloeziana* and *E. argophloia* for use in productivity models.

Eucalyptus cloeziana has a wide natural distribution, occurring in four disjunct geographical regions in Queensland: southern coastal, southern inland, northern coastal and northern inland, from sea level to 1000 m altitude (Turnbull 1979). These areas have a warm humid to subhumid climate, with mean maximum temperature of the hottest month between 29 and 34°C and mean minimum of the coldest month ranging between 5 and 18°C and annual rainfall between 550 and 2300 mm (Boland *et al*. 1984). The natural distribution of *E. argophloia* occurs in a narrow range in the south-western part of Queensland, at sites with a mean maximum temperature of the hottest month of 32°C and the mean minimum of the coldest month of 4°C (Boland *et al.* 1984). These sites usually have 10–15 frost days per year and an altitude of about 300 m. There is dearth of information on the silviculture of these two species in Queensland.

The aim of this study was to investigate the effects of temperature changes on the potential for photosynthetic assimilation, and to characterise the shape of light response curves at different temperatures. It was hypothesised (1) that *E. cloeziana* and *E. argophloia* survive extreme temperature fluctuations because of their ability to acclimate photosynthesis and respiration and (2) that there are no significant differences in the degree of acclimation and quantum yield between the dry- and wet-provenance *E. cloeziana* and *E. argophloia*. The specific objectives were to characterise the nature of the photosynthetic light and temperature response curves, and the effect of short-term (1–4 days) and long-term (4 months) temperature acclimation on net photosynthesis in the leaves of *E. cloeziana* (dry and wet provenances) and *E. argophloia* seedlings.

Materials and methods

Seedlings of a humid-provenance *E. cloeziana* from Gympie, of a dry-zone provenance *E. cloeziana* from Hungry Hills and of *E. argophloia* from Ballon (Table 1) were raised in pots containing a 50 : 50 mixture of peat and vermiculite at the Queensland Forestry Research Institute Gympie (QFRI). In June 2000, the 6-month-old seedlings were moved to a University of Queensland glasshouse (Brisbane) and transferred into plastic pots (175 mm diameter × 175 mm deep) containing nursery top soil (loam-textured) mixed with vermiculite and perlite in the ratio of 4 : 1 : 1. Slow-release fertiliser [Osmocote Plus (3–4 months) containing micronutrients] was mixed with the potting medium at a rate of 2 kg m^{-3}. The pots were well-watered and maintained in a naturally lit glasshouse, with temperature control provided by evaporative coolers and electric fan heaters. In mid-January 2001, 12 plants of each provenance were transferred into 5-L pots containing similar potting medium and maintained in similar conditions for 2 weeks to recover before being moved to controlled-temperature glasshouses.

Photosynthetic response to light

At the beginning of February 2001, three plants of each provenance were acclimated in naturally lit controlled-temperature glasshouses at day/night temperatures of 18/13, 23/18, 28/23 and 33/28°C. Plants were left to equilibrate overnight at each temperature before light-response data were collected. Plants were watered twice per day and supplied with complete nutrient solution weekly. Measurements of gas exchange in February 2001 were made using a CIRAS infrared analyser equipped with a Parkinson leaf chamber (PP Systems, HertfordShire, England), whereas in June 2001 gas exchange was measured using a LI-6400 portable photosynthesis system (Li-Cor, Inc., Lincoln, NE) equipped with a 6400–02B LED light source installed above the leaf chamber. Rapid light response curves were derived from data collected at 2000, 1500, 1000, 800, 550, 350, 200, 100, 25 and 0 μmol m^{-2} s^{-1}. At each step, the leaf was left to equilibrate until CO_2 flux was constant (3–5 min). Relative humidity in the controlled-temperature glasshouse was maintained at between 50 and 80% by using an automatic electric steam humidifier (Hankscraft, Dion, Gerber Inc., Canada). Measurements were taken at ambient CO_2 concentration and vapour pressure deficit at the leaf surface was kept below 1.5 kPa. The second set of light response curves was derived in Jun 2001 concurrent with temperature acclimation response and after the plants had acclimated to the particular growth conditions for 4 months.

Photosynthetic response to temperature

Similar measurement conditions as those used for light-response measurements were maintained during temperature acclimation measurements. Only the young fully formed leaves that had developed at each acclimation temperature were used for gas exchange measurements. An incident PPFD of 1500 μmol m^{-2} s^{-1} (fully saturating) was maintained at the leaf surface. Measurement of gas exchange was undertaken at the particular temperature at which the plants had been acclimated between 0800 and 1100 hours. Initial measurements of gas exchange in February 2001, 3 days after the plants were moved to the respective controlled temperature, were measured with CIRAS infrared gas analyser, whereas LI-6400 portable photosynthesis system was used for the June 2001 observations.

At each growth temperature, photosynthesis was measured at leaf temperatures ranging from 13 to 43°C, using light-, humidity- and temperature-control options of the LI-6400. During most measurements, vapour pressure deficit at the leaf surface was kept below 2.0 kPa; however, it was not possible to maintain vapour pressure deficit at this level at leaf temperatures above 35°C. Owing to the inherent cooling limitations of LI-6400 leaf chamber, leaf temperature could not be reduced more than 10°C below ambient. Warming was more efficient and could be increased to 50°C. Consequently, for plants grown at 33°C, leaf temperature was first increased to 43°C, then the leaf was removed from the chamber and left to equilibrate for 10 min. The temperature of the leaf was then decreased at a pace of approximately 0.5°C min^{-1}, and measurements taken at 5°C intervals. For plants grown at 18°C, leaf temperature was reduced to 13°C and then increased gradually at a similar pace (Ferrar *et al.* 1989). Leaves were maintained at a specified temperature for 5–10 min before gas exchange readings were taken. For plants grown at 28 and 33°C, low temperatures were achieved by moving plants to the 23 or 18°C glasshouses 2 h before the measurement of gas exchange and then returned to their growth environment.

Modelling light and temperature response

Light response curves of photosynthesis are initially linear with a slope corresponding to the maximum quantum yield of photosynthesis. At high quantum flux, there is a progressive convexity that leads to an asymptote and light-saturated rate of CO_2 uptake (Long and Hällgren 1993). A non-rectangular hyperbolic function (Baker *et al.* 1988; Long and Hällgren 1993; Pinkard and Beadle 1998) was used to describe the response of net photosynthesis to photon flux density:

$$A = 2\alpha Q A_{\max} / [aQ + A_{\max} + \sqrt{(aQ + A_{\max})^2 - 4\theta Q A_{\max}}] - rd, \quad (1)$$

where α, the slope of the linear phase, approximates the maximum quantum yield (photosynthetic efficiency); $A_{\max}$ is the light-saturated photosynthetic rate; θ describes the shape (convexity) of the light response curve; *rd* approximates leaf dark respiration; *A* is the net photosynthetic rate and *Q* is the photon flux density. At each growth temperature, the responses of CO_2 uptake to changes in temperature were described by curves resembling parabolas, with maximum at the optimum temperature (Säll and Pettersson 1994; Battaglia *et al.* 1996):

$$A(T) = A_{\mathrm{opt}} - b\,(T - T_{\mathrm{opt}})^2, \quad (2)$$

where $A(T)$ is the observed net photosynthetic rate at a measurement temperature T, A_{opt} is the rate of photosynthesis at optimum temperature T_{opt} and *b* is a positive factor that determines the width of parabola. The relationship between growth temperature and optimum temperature was described by a linear function as shown for *E. pauciflora* (Slatyer and Ferrar 1977*a*):

$$T_{\mathrm{opt}} = T_{\mathrm{pref}} + \alpha(T_{\mathrm{eff}} - T_{\mathrm{pref}}), \quad (3)$$

where T_{opt} is the observed optimum temperature, T_{pref} is the preferred temperature which is defined as the temperature at which optimum temperature coincides with the growth temperature, T_{eff} is the temperature at which the plants were acclimated and α, the slope of the regression line, is the acclimation coefficient which represents the extent of acclimation as described by Slatyer and Ferrar (1977*a*) and Säll and Pettersson (1994), where $\alpha = 1$ indicates complete acclimation and $\alpha < 1$ indicates incomplete acclimation or an inability of the plant to make optimal response.

Results

Light response curves

At each acclimation temperature and ambient CO_2 concentration, PPFD greater than 900 μmol m^{-2} s^{-1} was saturating for each provenance and was not influenced by the duration of acclimation (see Fig. 1—plants measured in February 2001; Fig. 2—plants measured in June 2001). There were no significant differences in the shape and quantum-yield parameters among plants of different provenances at the 23, 28 and 33°C growth temperatures. However, at 18°C, the shape parameter of *E. argophloia* (0.42) was significantly smaller than those for plants of the two *E. cloeziana* provenances, which did not differ significantly from each other (average of 0.69). The values for quantum yield at 23, 28 and 33°C varied between 0.04 and 0.06 μmol CO_2 μmol^{-1} PPFD. The quantum-yield parameter of *E. argophloia* at 18°C was significantly greater (0.06) than that of the humid-provenance *E. cloeziana* (0.04). There were no significant differences in the values of shape and quantum-yield parameters of the light response curves at any of the four growth temperatures (18, 23, 28 and 33°C) within each provenance (Table 2). The values of the shape parameter varied from 0.71 to 0.78 for the humid-provenance *E. cloeziana*, from 0.62 to 0.71 for the dry-provenance *E. cloeziana* , and from 0.42 to 0.60 for *E. argophloia*.

Differences among provenances in $A_{\max}$ were observed at the 18°C growth temperature, where $A_{\max}$ values for

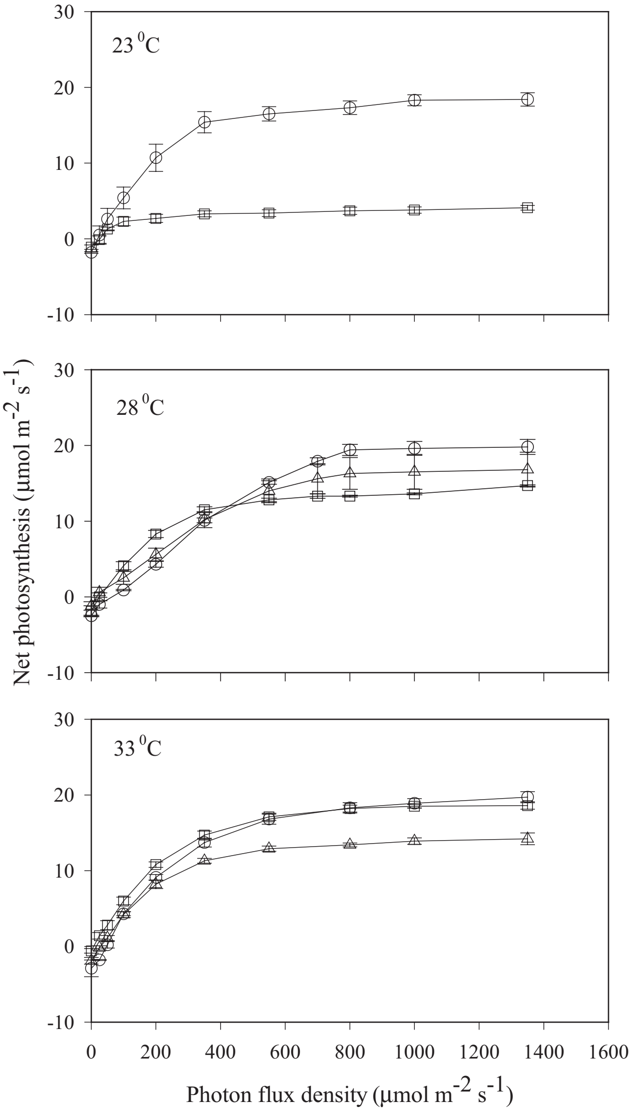

Fig. 1. Photosynthetic light response curves of young fully expanded leaves of *Eucalyptus argophloia* (circles) and a humid (squares) and dry (triangles) provenance of *E. cloeziana* at 23, 28 and 33°C. All measured at >60% relative humidity and ambient CO_2 (340 µmol m^{-2} s^{-1}) in February 2001.

E. argophloia and the dry-provenance *E. cloeziana* were higher than that for the humid-provenance *E. cloeziana* (Table 2). However, there were no significant differences in A_{max} among the three provenances at 23, 28 and 33°C acclimation temperatures. At 18°C, the dark-respiration rates for plants of both provenances of *E. cloeziana* were significantly lower than that of *E. argophloia*. For both provenances of *E. cloeziana*, values of A_{max} and dark respiration at 28 and 33°C were significantly higher than those at 18 and 23°C (Table 2). The A_{max} values observed for these provenances were 16.2 µmol m^{-2} s^{-1} for the humid- and 21.4 µmol m^{-2} s^{-1} for the dry-provenance *E. cloeziana*, and 18.6 µmol m^{-2} s^{-1} for *E. argophloia*. For each provenance,

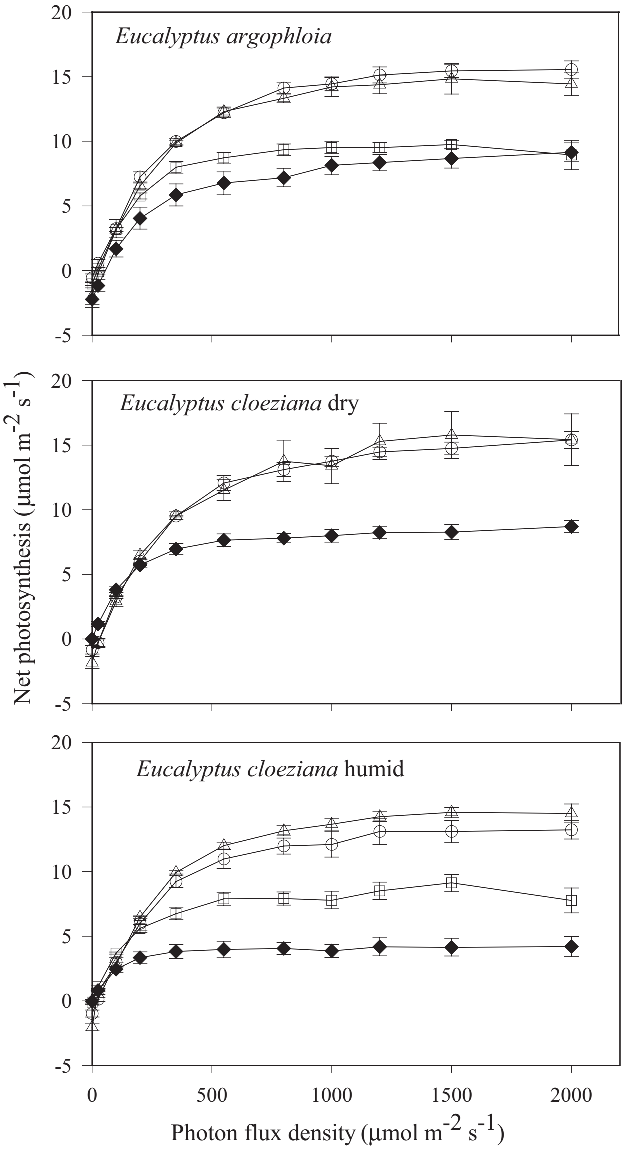

Fig. 2. Light response curves of young fully expanded leaves of *Eucalyptus argophloia* and a dry and humid provenance of *E. cloeziana* at 18°C (diamonds), 23°C (squares), 28°C (triangles) and 33°C (circles). Measurements were taken at >60% relative humidity and ambient CO_2 (340 µmol m^{-2} s^{-1}) in June 2001, after a 4-month acclimation period.

there were no significant differences in the light-saturated photosynthetic rates (A_{max}) between 18 and 23°C, and between 28 and 33°C growth temperatures, but A_{max} values were higher at the higher temperatures (Fig. 3).

There was no consistent trend in the response of dark respiration measured at the growth temperatures (18, 23, 28 and 33°C) for each provenance. When measured at 18°C, *E. argophloia* plants had a significantly greater respiration rate (2.33 µmol m^{-2} s^{-1}) than those of either of the *E. cloeziana* provenances (0.02 µmol m^{-2} s^{-1}). However, there were no significant differences in respiration among

Table 2. Among-provenance comparison of the apparent quantum yield (Φ, μmol CO_2 μmol^{-1} PAR), shape of light curve (θ), light-saturated photosynthetic rate (A_{max}, μmol m^{-2} s^{-1}) and leaf dark-respiration rate (*rd*, μmol m^{-2} s^{-1}) of plants measured at four growth temperatures and ambient CO_2 (340 μmol mol^{-1}) in June 2001

At each temperature, letters in a column indicate differences among provenances at $P = 0.05$

Temperature (°C)	Provenance	θ	Φ	A_{max}	*rd*
18	*E. cloeziana* humid	0.73a	0.04b	4.33c	–0.03a
	E. cloeziana dry	0.65a	0.05ab	8.67b	0.01a
	E. argophloia	0.42b	0.06a	12.34a	–2.33b
23	*E. cloeziana* humid	0.71	0.05	8.74	–0.15
	E. cloeziana dry	—	—	—	—
	E. argophloia	0.68	0.05	11.44	–1.07
28	*E. cloeziana* humid	0.78	0.05	16.2	–1.69
	E. cloeziana dry	0.62	0.05	21.38	–1.89
	E. argophloia	0.70	0.05	18.62	–1.99
33	*E. cloeziana* humid	0.76	0.04	14.43	–0.94
	E. cloeziana dry	0.71	0.05	17.10	–1.08
	E. argophloia	0.60	0.05	17.53	–0.61

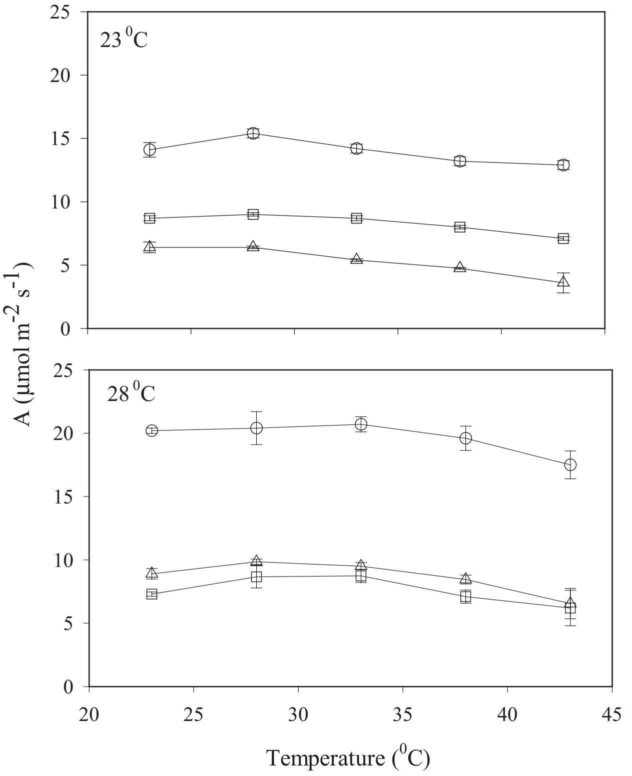

Fig. 3. The effect of growth temperature on the net photosynthetic rates (*A*) of the humid (squares) and dry (triangles) provenances of *Eucalyptus cloeziana* and *E. argophloia* (circles) measured at 23 and 28°C growth regimes after 3 days of acclimation in February 2001.

provenances at 23, 28 and 33°C. The dark-respiration rate varied between 0.03 and 1.69 μmol m^{-2} s^{-1} for the humid-provenance *E. cloeziana*, between 0.01 and 1.89 μmol m^{-2} s^{-1} for the dry-provenance *E. cloeziana*, and between –0.61 and 2.33 μmol m^{-2} s^{-1} for *E. argophloia*.

Temperature response curves

The photosynthetic temperature response curves of *E. argophloia* plants and those of the two provenances of *E. cloeziana*, measured after plants had been acclimated at 23 and 28°C in controlled-temperature glasshouses for 3 days, were broad, slightly asymmetric and lacking clear optima (Fig. 3). The optimum temperatures for net photosynthesis were more closely related to the mean daily temperature of the 5 days preceding the transfer of plants to the controlled-temperature glasshouse than to the day-time temperatures in the controlled-temperature glasshouse (Fig. 3). *E. argophloia* showed higher rates of photosynthesis at both 23 and 28°C acclimation temperatures than did *E. cloeziana* plants from either of the two provenances. Plants from the two provenances of *E. cloeziana* differed only slightly at 28°C, while at 23°C the dry-provenance plants showed lower rates of photosynthesis than did the humid-provenance plants. In both species, the maximum rate of photosynthesis was lower at 23°C than that at 28°C (Fig. 3).

Temperature response curves of net photosynthesis for plants of the three provenances after 4 months of acclimation were similar in form, showing little response to temperatures between 28 and 38°C (Fig. 4). Since it was not possible to maintain vapour pressure deficit below 2.0 kPa over the entire temperature range, the response of net photosynthesis above 35°C may have been compounded by changes in stomatal conductance. At 18 and 23°C, *E. argophloia* plants showed higher rates of photosynthesis than did those of the two provenances of *E. cloeziana*, which showed leaf rolling in response to cold temperature and limited response to changes in temperature (Fig. 4). At 28°C growth regime, the dry-provenance *E. cloeziana* plants showed higher rates of photosynthesis between 28 and 38°C than did the *E. argophloia* and the humid-provenance *E. cloeziana*

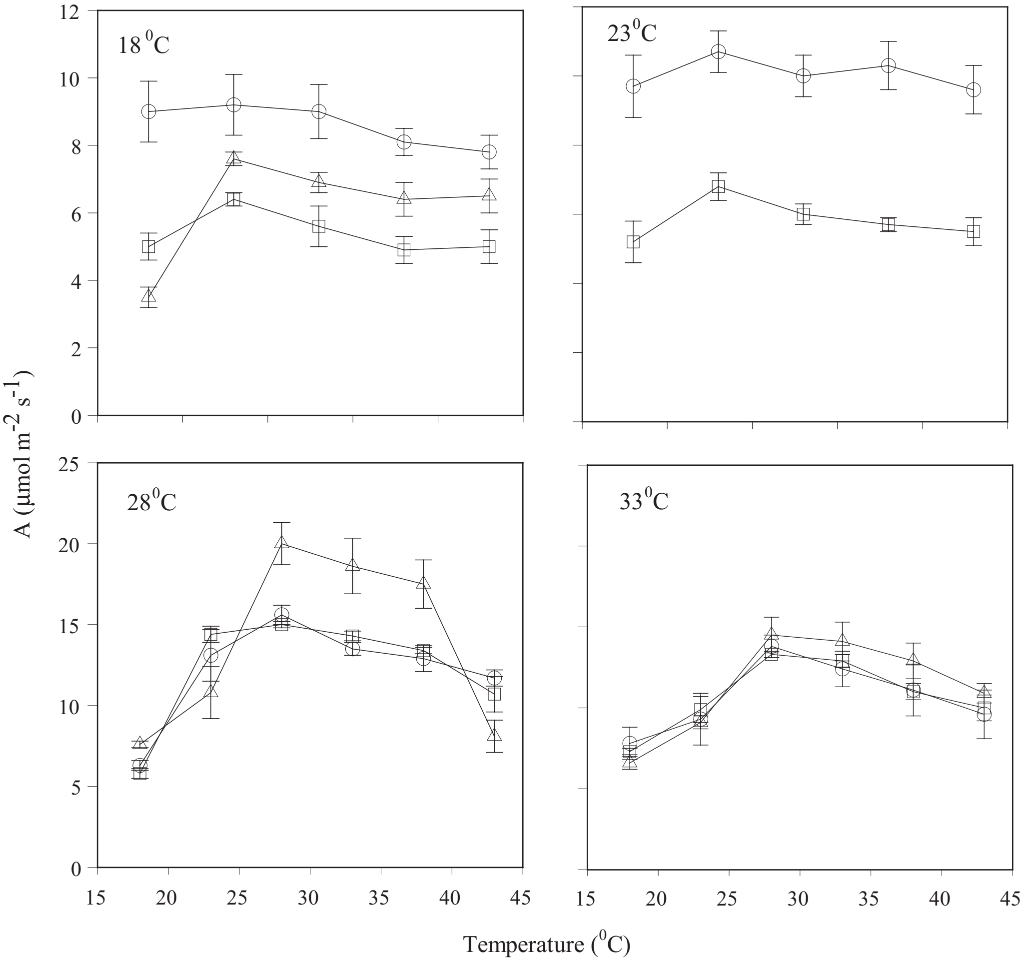

Fig. 4. Response of net photosynthesis (*A*) of the humid (squares) and dry (triangles) provenances of *Eucalyptus cloeziana*, and *E. argophloia* (circles) to temperature. Measurements were made at 18, 23, 28 and 33°C controlled-temperature glasshouses, at >60% relative humidity and ambient CO_2 (340 µmol m^{-2} s^{-1}) in June 2001, after a 4-month acclimation period.

plants, which were very similar. This large difference was associated with some young highly active leaves. The photosynthetic rates for the three provenances at 33°C were very similar (Fig. 4).

Eucalyptus argophloia grown at 18 and 23°C showed higher stomatal conductance at lower leaf temperatures than did plants of either provenance of *E. cloeziana*. There were similar responses in stomatal conductance between *E. argophloia* and the humid-provenance *E. cloeziana* at 28°C, but stomatal conductance of the dry-provenance plants peaked close to the acclimation temperature (Fig. 5). There were minor differences among provenances in stomatal response at 33°C. Decreased stomatal conductance with increased temperature was associated with increased vapour pressure deficit.

The responses of net photosynthesis to temperature for plants of the three provenances were described using a parabola of the form described by Equation 2, and parameters presented in Table 3 for each acclimation temperature. The shape parameter (*b*) for the three provenances at 18 and 23°C was not significantly different from zero, rendering it unsatisfactory; however, the parameter was reliable for all provenances at 28 and 33°C as shown by the shape of response curves in Fig. 4. The optimum temperature for photosynthesis increased from 23 to 32°C (9°C) for the humid- and from 25 to 33°C (8°C) for the dry-provenance *E. cloeziana*, and from 21 to 33°C (12°C) for *E. argophloia* as the growth temperature increased from 18 to 33°C (Table 3). The optimum temperature at which A_{max} was observed was linearly and positively correlated with the growth temperature (T_{eff}) (Fig. 6), and the acclimation coefficient (α), as depicted by Equation 3, was highest for *E. argophloia* (α = 0.72), followed by the dry- (α =0.59) and the humid-provenance (α = 0.28) *E. cloeziana*. Consequently, the highest degree of acclimation was found in *E. argophloia*, whereas the lowest was observed in the humid-provenance *E. cloeziana*.

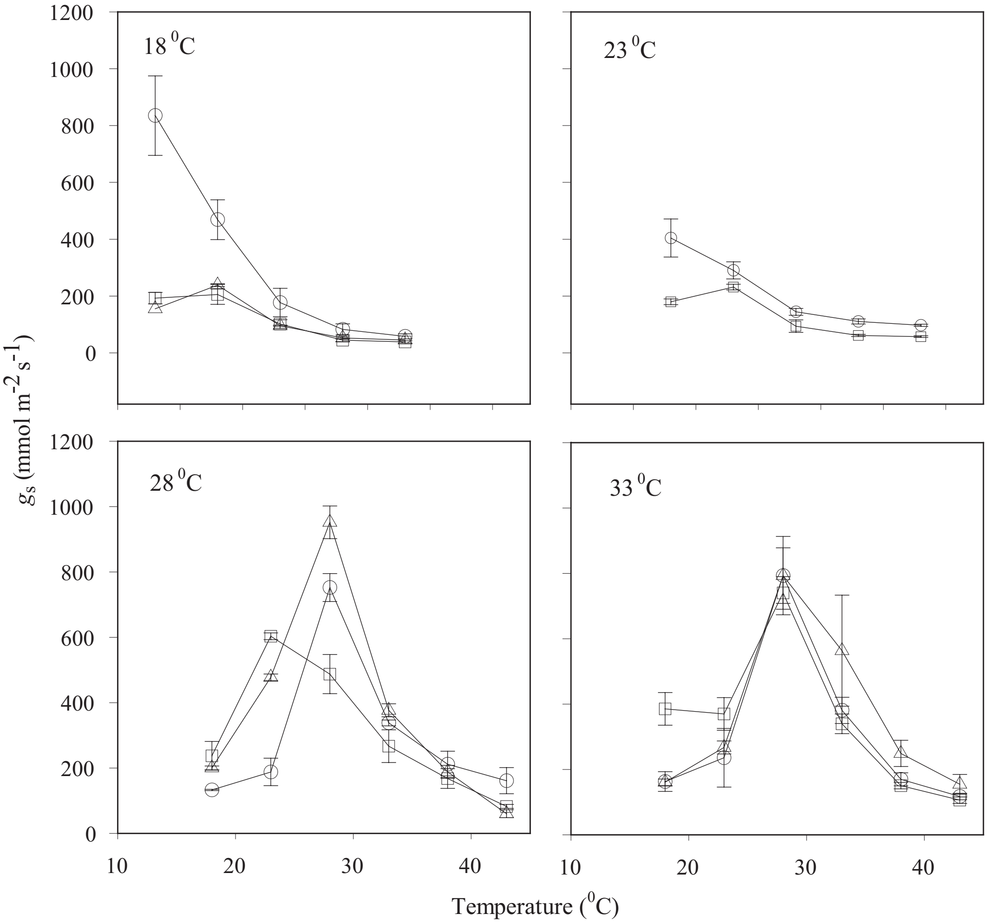

Fig. 5. Response of stomatal conductance (g_s) of the humid (squares) and dry (triangles) provenance of *Eucalyptus cloeziana*, and of *E. argophloia* (circles) to temperature. Measurements were made at 18, 23, 28 and 33°C controlled-temperature glasshouses in June 2001.

Table 3. hotosynthetic response curves as defined by a parabolic function $A(T) = A_{opt} - b(T - T_{opt})^2$, where A is the rate of photosynthesis at temperature T, A_{opt} is the maximum photosynthesis at optimum temperature T_{opt}, b describes the spread of the parabola and T_{eff} is the growth temperature

Standard errors are given in parentheses

Taxonomic provenance	T_{eff} (°C)	A_{opt} (μmol m^{-2} s^{-1})	b	T_{opt} (°C)
E. cloeziana humid	18	7.03 (0.68)	0.021 (0.010)	23.4 (2.0)
	23	6.55 (0.43)	0.013 (0.001)	28.9 (0.5)
	28	15.60 (0.07)	0.045 (0.004)	32.0 (0.4)
	33	12.55 (0.54)	0.027 (0.001)	31.9 (0.6)
E. cloeziana dry	18	7.50 (0.040)	0.023 (0.001)	24.8 (0.6)
	28	12.61 (0.72)	0.029 (0.002)	32.3 (1.1)
	33	14.11 (1.03)	0.034 (0.005)	33.2 (0.1)
E. argophloia	18	10.07 (0.7)	0.020 (0.004)	20.9 (1.5)
	23	10.39 (1.19)	0.015 (0.005)	28.6 (0.2)
	28	14.43 (0.57)	0.035 (0.001)	33.4 (0.1)
	33	13.59 (1.61)	0.035 (0.004)	31.2 (0.3)

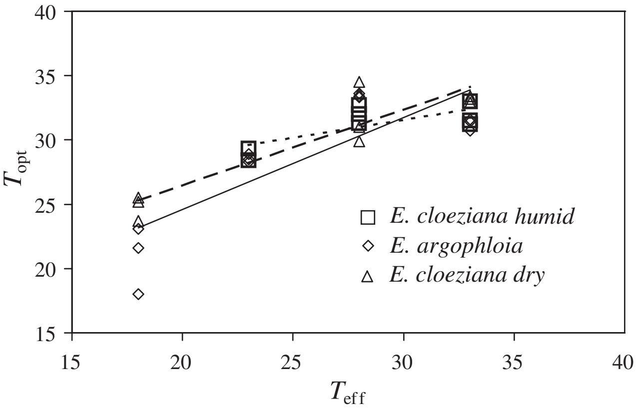

Fig. 6. The relationship between optimum temperature, T_{opt} (temperature at which maximum photosynthesis was observed) and the temperature of the growth environment (T_{eff}) for the three provenances. Equations for the lines (see formulation of Eqn 3) were T_{opt}=32.2 – 0.28(32.2 – T_{eff}), r^2 = 0.54, for the humid (dashed line) and T_{opt} = 35.7 – 0.59(35.7 – T_{eff}), r^2 = 0.84, for the dry (broken line) provenances of *Eucalyptus cloeziana*, and T_{opt} = 36.2 – 0.72(36.2 – T_{eff}), r^2 = 0.68, for *E. argophloia* (continuous line). The intersection point of the curves and the line with a slope of one represents the preferred temperature.

The value of preferred temperature (T_{pref}) for the humid-provenance *E. cloeziana* (32.2°C) was closer to the optimum temperature for photosynthesis attained at growth temperatures 28 and 33°C (Fig. 6 and Table 3). However, the value for T_{pref} for the dry-provenance *E. cloeziana* (35.7°C) was 3°C higher than the optimum temperature attained at 33°C. T_{pref} of *E. argophloia* (36.2°C) was 3°C higher than the optimum attained at 28°C.

Discussion

The shapes of light response curves and the magnitudes of quantum yield of *E. cloeziana* and *E. argophloia* plants grown in glasshouses under different temperature regimes (18–33°C day temperatures) were not affected by temperature. However, the photosynthetic temperature optima of the two species were markedly affected by the temperature at which the plants had been acclimated for 4 months, whereas there was little evidence of photosynthetic acclimation when plants were exposed to a growth environment for 3 days. These results supported the hypothesis that plants of these three provenances cope with extreme temperature fluctuations because of their capacity to acclimate gradually to the prevailing temperature conditions, but did not support the hypothesis that the shape of light response curve and the magnitude of quantum yield change with temperature. The capacity to acclimate to changes in temperature is consistent with the ecological data for the species that indicate a wide seasonal variability in temperature (Table 1).

Light response curves for each provenance and at each growth temperature were adequately defined by a non-rectangular parabola as has been reported for *E. nitens* (Pinkard and Beadle 1998). Growth temperature affected the light-saturated photosynthetic rates of plants of all provenances grown at 23, 28 and 33°C, and measured at the same temperatures, but did not affect quantum yield. In another C_3 species, *Encelia californica*, plants grown in light and temperature conditions within their normal range maintained their quantum yield (Ehleringer and Pearcy 1983). Quantum yields for all provenances did not differ significantly at 23, 28 and 33°C and ranged between 0.04 and 0.06, whereas at 18°C the quantum yield of *E. argophloia* was greater than that of the humid-provenance *E. cloeziana*. These values compare with the range of 0.05–0.06 reported for a large number of C_3 dicotyledonous species (Ehleringer and Björkman 1977; Ehleringer and Pearcy 1983), the range from 0.02 in winter to 0.06 in summer for *Pinus sylvestris* (L.) (Leverenz and Öquist 1987), the range of 0.04–0.06 for *E. nitens* (Pinkard and Beadle 1998) and 0.05 for *E. globulus* (Battaglia and Sands 1997); but were higher than the average value for maximum canopy quantum efficiency of 0.03 mol C mol^{-1} photon obtained for a mixed forest of conifers and deciduous hardwoods at Harvard Forest in central Massachusetts (Waring *et al.* 1995).

The shapes of the light response curves for *E. argophloia* and *E. cloeziana* of the two provenances were similar at 23, 28 and 33°C, with curvature values ranging from 0.53 to 0.78. Leverenz (1988) found no evidence of temperature effects on the shape of a single-leaf light response curve, but reported effects of temperature on A_{max} and quantum yield. The A_{max} values of plants did not differ significantly among the three provenances at 23, 28 and 33°C, but were highest at 28 and 33°C growth temperatures. The highest values of A_{max} were 21.38 µmol m^{-2} s^{-1} for the dry- and 16.2 µmol m^{-2} s^{-1} for the humid-provenance *E. cloeziana*, and 18.6 µmol m^{-2} s^{-1} for *E. argophloia*. These values are slightly higher than those (14.35–15.7 µmol m^{-2} s^{-1}) reported for 4-year-old trees of *E. globulus* (Battaglia *et al.* 1996), but lower than the range of 23.4–29.5 µmol m^{-2} s^{-1} reported for 1-year-old trees of *E. nitens* (Pinkard and Beadle 1998). In the lowest temperature regime (18°C), the A_{max} of *E. argophloia* was significantly higher than that of the dry-provenance *E. cloeziana*, while that of the humid-provenance *E. cloeziana* was the lowest.

Interpretation of the response of dark respiration to growth-regime temperature for each provenance was obscured by the variability of the response (Table 2). The average values (–0.61 to –1.86 µmol m^{-2} s^{-1}) were much lower than the range of –3.01 to –2.87 µmol m^{-2} s^{-1} reported for 1-year-old *E. nitens* plants grown in Tasmania and measured in summer (Pinkard and Beadle 1998). However, the values in this study are consistent with those reported for

Pinus taeda seedlings raised in growth chambers (Teskey and Will 1999) and those reported for *E. globulus* in Portugal during summer (Pereira *et al.* 1986).

The photosynthetic temperature optima for *E. cloeziana* and *E. argophloia* approached the day-time temperatures of their growth environments. Similarly, rates of net photosynthesis shifted with the measurement temperature such that the highest values were observed close to the temperature at which the plants were grown (Fig. 4). Temperature response curves (Fig. 4) for plants of both *E. cloeziana* provenances and for *E. argophloia* at 28 and 33°C growth temperature were broadly parabolic and symmetrical around the optimum temperature, unlike the smooth unimodal curves described by Säll and Pettersson (1994). This poor fit was partly associated with values obtained after moving plants to a different room temperature (Teskey and Will 1999). The optimum temperature shifted by 9°C for the humid- and 8°C for the dry-provenance *E. cloeziana*, and 12°C for *E. argophloia* as the growth temperature increased from 18 to 33°C (Table 3). In the field-grown *E. globulus*, the optimum temperature for net photosynthesis increased from 17 to 23°C as the mean daily temperature increased from 7 to 16°C, and in *E. nitens* temperature optimum increased from 14 to 20°C as the mean daily temperature increased from 7 to 19°C (Battaglia *et al.* 1996). These results provide evidence of acclimation and are consistent with those reported for *P. taeda* (Teskey and Will 1999), *E. pauciflora* (Slatyer 1977*b*), *Nothofagus* species (Read 1990), *E. globulus* (Battaglia *et al.* 1996), *Larix decidua* Mill. (Tranquillini *et al.* 1986) and *Eucalyptus* species and *Nerium oleander* (Ferrar *et al.* 1989) under controlled-temperature environments, and in field-grown trees (Strain *et al.* 1976; Slatyer 1977*a*; Slatyer and Marrow 1977; Battaglia *et al.* 1996).

After 3 days of acclimation at 23 and 28°C, temperature optima for plants of the three provenances were higher than the daytime temperature of the acclimation condition (Fig. 3) but lower than a 5-day temperature average (37°C) of their previous growth environment as suggested by Battaglia *et al.* (1996), indicating some degree of buffering. Similar results have been reported for *E. pauciflora* on Day 2 after transferring plants from field to controlled-temperature glasshouses (Slatyer and Ferrar 1977*a*).

The slope (α, acclimation coefficient) of the linear relationship between optimum temperature for net photosynthesis and growth temperature (Equation 3; Fig. 6) for plants of each provenance indicates that relative to complete acclimation (α = 1) (Säll and Pettersson 1994), *E. argophloia* (α = 0.72) acclimated more than the dry-provenance (α = 0.59) and humid-provenance (α = 0.25) of *E. cloeziana*. These slopes indicate a change of 1 degree in temperature optimum for each change in growth temperature of 1.4 degrees for *E. argophloia*, 1.7 degrees for dry-provenance *E. cloeziana* and 4 degrees for humid-provenance *E. cloeziana*. The observed slopes suggest that shifts of seasonal degrees in the temperature optimum can be expected in relation to seasonal temperature changes under field conditions (Slatyer 1977*b*). Moreover, the acclimation coefficients for *E. cloeziana* are comparable to those reported for *E. globulus* (α = 0.59) and *E. nitens* (α = 0.35) in the field (Battaglia *et al.* 1996), and the range of 0.295–0.356 reported for *E. pauciflora* (Slatyer 1977*b*), but are lower than that for *E. argophloia*.

The humid-provenance *E. cloeziana* studied here originated from a coastal environment with a mean minimum temperature of the coldest month of 5.3°C and the mean maximum temperature of the warmest month of 30.6°C (Table 1), while the dry-provenance plants originated from an inland environment with the mean minimum temperature of the coldest month of 7.2°C and the mean maximum temperature of the warmest month of 30.0°C. The limited differences in photosynthetic temperature acclimation response of plants of the humid and the dry provenances of *E. cloeziana* may be related to the temperature similarity at the place of origin of each provenance. Moreover, broad photosynthetic optima observed for these two provenances are often found in taxa from variable environments (Read 1990; Battaglia *et al.* 1996). Nevertheless, the preferred temperature at which the optimum temperature coincides with the growth temperature was higher for the dry-provenance (35.7°C) than for the humid-provenance (32.2°C) *E. cloeziana*, suggesting their greater ability to tolerate high temperatures, while the preferred temperature for the humid-provenance *E. cloeziana* was similar to that reported for *E. globulus* (32.3°C) (Battaglia *et al.* 1996).

Eucalyptus argophloia originated from an inland environment with the mean minimum temperature of the coldest month of 3.7°C and the mean maximum temperature of the warmest month of 32°C (Table 1). Plants from habitats with large temperature variations during growing season, as observed for *E. argophloia*, tend to possess a greater potential for acclimation over a wide temperature range than do plants from habitats with relatively stable temperatures during periods of active growth (Berry and Björkman 1980). *E. argophloia* also experiences more frost days (10–15) per year than does *E. cloeziana*, with about five light frosts per year expected for the latter species throughout its range of natural distribution (Boland *et al.* 1984). Thus, the ability of *E. argophloia* to maintain a substantial photosynthetic rate at cool temperatures (<23°C) and a higher preferred temperature (36.2°C) are consistent with its tolerance to low minimum temperatures of the coldest month, frequent frosts and higher maximum temperatures than those for *E. cloeziana* provenances.

The results of this study have shown that photosynthetic temperature optimum of the humid- and dry-provenance *E. cloeziana* and of *E. argophloia* could be shifted several degrees by acclimation to contrasting growth-temperature regimes, and also that different provenances yield different temperature optima consistent to their ecological amplitude. The evidence suggests that photosynthetic temperature acclimation is one of the mechanisms enabling plants of these provenances to maintain active growth during warm summer months and cold winter months. However, plants of all three provenances lacked the ability to acclimate completely to the growth temperature, even though a pronounced shift in optimum temperature occurred. There are no major differences among plants of the three provenances in photosynthetic response at temperatures ranging from 28 to 43°C; however, plants of the two provenances from subhumid environment (*E. argophloia* and dry-provenance *E. cloeziana*) maintained higher photosynthetic rates at low temperatures (<23°C) than did plants of the humid provenance (Table 2). Moreover, it is possible that some potential differences among provenances were masked by the abundant water supply maintained during the study, as indicated by high transpiration rates (Fig. 5). The generally poor fit of the response curves of the two species to the Säll and Pettersson (1994) model is associated with the combination of methods used to generate the response curves, and species intrinsic responses to changes in temperature. These results have implications for predicting survival and productivity of *E. cloeziana* and *E. argophloia* saplings in areas outside their natural distributions. However, the use of these results to infer the functioning of older trees must proceed with caution and should be substantiated with field measurements from canopies (Waring *et al.* 1995; Law *et al.* 2000*a*; Law *et al.* 2000*b*; Lai *et al.* 2002).

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References

Baker NR, Long SP, Ort DR (1988) Photosynthesis and temperature, with particular reference to effects on quantum yield. In 'Symposia of the Society for Experimental Biology. Number XXXXII. Plants and temperature'. University of Essex, England. (Eds SP Long, FI Woodward) pp. 347–375. (The Company of Biologists Ltd: University of Cambridge)

Battaglia M, Sands P (1997) Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. *Australian Journal of Plant Physiology* **24**, 831–850.

Battaglia M, Beadle C, Loughhead S (1996) Photosynthetic temperature response of *Eucalyptus globulus* and *Eucalyptus nitens. Tree Physiology* **16**, 81–89.

Berry J, Björkman O (1980) Photosynthetic response and adaptation of temperature in higher plants. *Annual Review of Plant Physiology* **31**, 491–543. doi:10.1146/ANNUREV.PP.31.060180.002423

Bureau of Meteorology (2002) Bureau of Meteorology, Australia. Commonwealth of Australia, [Canberra]. http://www.bom.gov.au/climate

Björkman O, Badger MR, Armond PA (1980) Responses and adaptations of photosynthesis to high temperature. In 'Adaptations of plants to water and high temperature stress'. (Eds NC Turner, PJ Kramer) pp. 233–249. (J.Wiley & Sons: New York)

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)

Ehleringer J, Björkman O (1977) Quantum yields for CO_2 uptake of C_3 and C_4 plants dependence on temperature, CO_2 and O_2 concentration. *Plant Physiology* **59**, 86–90.

Ehleringer J, Pearcy RW (1983) Variation in quantum yield for CO_2 uptake among C_3 and C_4 plants. *Plant Physiology* **73**, 555–559.

Ferrar PJ, Slatyer RO, Vranjic JA (1989) Photosynthetic temperature acclimation in *Eucalyptus* species from diverse habitats, and a comparison with *Nerium oleander. Australian Journal of Plant Physiology* **16**, 199–217.

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.

Lai C-T, Katul G, Butnor J, Siqueira M, Ellsworth D, Maier C, Johnsen K, Mckeand S, Oren R (2002) Modelling the limits on the reponse of net carbon exchange to fertilization in a south-eastern pine forest. *Plant, Cell & Environment* **25**, 1095–1119. doi:10.1046/J.1365- 3040.2002.00896.X

Law BE, Waring RH, Anthoni PM, Aber JD (2000*a*) Measurements of gross and net ecosystem productivity and water vapour exchange of *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology* **6**, 155–168. doi:10.1046/J.1365-2486.2000.00291.X

Law BE, Williams M, Anthoni PM, Baldocchi DD, Unsworth MH (2000*b*) Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biology* **6**, 613–630. doi:10.1046/J.1365-2486.2000.00339.X

Leverenz JW (1988) The effects of illumination sequence, CO_2 concentration, temperature and acclimation on the convexity of the photosynthetic light response curve. *Physiologia Plantarum* **74**, 332–341.

Leverenz JW, Öquist G (1987) Quantum yields of photosynthesis at temperatures between –2 and 35°C in a cold tolerant C_3 plant (*Pinus sylvestris*) during the course of one year. *Plant, Cell & Environment* **10**, 287–295.

Long SP, Hällgren JE (1993) 'Measurement of CO_2 assimilation by plants in the field and the laboratory: field and laboratory manual.' (Chapman & Hall: London)

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.

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

Pereira JS, Tenhunen JD, Lange OL, Beyschlag W, Meyer A, David MM (1986) Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. *Canadian Journal of Forest Research* **16**, 177–184.

Pinkard EA, Beadle CL (1998) Regulation of photosynthesis in *Eucalyptus nitens* (Deane & Maiden) Maiden following green pruning. *Trees—Structure and Function* **12**, 366–376. doi:10.1007/S004680050163

Read J (1990) Some effects of acclimation temperature on net photosynthesis in some extra-tropical Australasian *Nothofagus* species. *Journal of Ecology* **78**, 100–112.

Säll T, Pettersson P (1994) A model of photosynthetic acclimation as a special case of reaction norms. *Theoretical Biology* **166**, 1–8. doi:10.1006/JTBI.1994.1001

Slatyer RO (1977*a*) Altitudinal variation in the photosynthetic characteristics of *Eucalyptus pauciflora* Sieb. ex Spreng. VI. Comparison of field and phytotron responses to growth temperature. *Australian Journal of Plant Physiology* **4**, 901–916.

Slatyer RO (1977*b*) Altitudinal variation in the photosynthetic characteristics of *Eucalyptus pauciflora* Sieb.ex spreng. IV. Temprature response of four populations grown at different temperatures. *Australian Journal of Plant Physiology* **4**, 583–594.

Slatyer RO, Ferrar PA (1977*a*) Altitudinal variation in the photosynthetic characteristics of *Eucalyptus pauciflora* Sieb. ex Spreng. V. Rate of acclimation to an altered environment. *Australian Journal of Plant Physiology* **4**, 595–609.

Slatyer RO, Ferrar PJ (1977*b*) Altitudinal variations in the photosynthetic characteristics of of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. II. Effect of growth temperature under controlled conditions. *Australian Journal of Plant Physiology* **4**, 289–299.

Slatyer RO, Marrow PA (1977) Altitudinal variations in the photosynthetic characteristics of of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. II. Seasonal changes under field conditions in the snowy mountains area of south-eastern Australia. *Australian Journal of Botany* **25**, 1–10.

Strain BR, Higginbotham KO, Mulroy JC (1976) Temperature preconditioning and photosynthetic capacity of *Pinus taeda* L. *Photosynthetica* **10**, 47–53.

Teskey RO, Will RE (1999) Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. *Tree Physiology* **19**, 519–525.

The 2020 Vision (1997) Plantations of Australia. Ministerial Council on Forestry, Fisheries and Aquaculture, Standing Committee on Forestry, Plantations Australia, Forest Growers, and the National Association of Forest Industries, AGPS, Canberra.

Tranquillini W, Havranek WM, Ecker P (1986) Effect of atmospheric humidity and acclimation temperature on the temperature response of photosynthesis in young *Larix decidua* Mill. *Tree Physiology* **1**, 37–45.

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

Waring RH, Law BE, Goulden ML, Bassow SL, McCreight RW, Wofsy SC, Bazzaz FA (1995) Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant, Cell & Environment* **18**, 1201–1213.

Weis E, Berry JA (1988) Plants and high temperature stress. In 'Symposia of the Society for Experimental Biology. Number XXXXII. Plants and Temperature'. University of Essex, England. (Eds SP Long, FI Woodward) pp. 329–346. (The Company of Biologists Ltd: University of Cambridge)

Xiong FS, Ruhland CT, Day TA (1999) Photosynthetic temperature response of the antarctic vascular plants Colobanthus quitensis and Deschampsia antarctica. *Physiologia plantarum* **106**, 276–286. doi:10.1034/J.1399-3054.1999.106304.X

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