

Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*

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Summary Steady-state photosynthetic responses to leaf temperature of 4-year-old *Eucalyptus globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden trees were measured between 10 and 35 °C at approximately monthly intervals from early spring to midwinter. The photosynthetic temperature optimum of recently expanded leaves in the sun canopy was linearly related to the average temperature of the preceding week during the 9-month measurement period. The optimum temperature for net photosynthesis of *E. globulus* increased from 17 to 23 °C as the mean daily temperature increased from 7 to 16 °C. Similarly, the optimum temperature for net photosynthesis of *E. nitens* increased from 14 to 20 °C as the mean daily temperature increased from 7 to 19 °C. The temperature for maximum photosynthetic response of *E. globulus* and *E. nitens* was similar at each measurement time, but the photosynthetic performance of *E. nitens* was less sensitive to temperatures above and below this optimum than that of *E. globulus*. In December, the apical shoots of branches of *E. globulus* had a net photosynthetic temperature optimum of between 10 and 15 °C. The corresponding values for expanding leaves, fully expanded leaves from the current year's growth, and fully expanded leaves from the previous year's growth were 15, 20 and 20–25 °C, respectively.

In a second experiment, *E. globulus* clones taken from four mother plants originating from climatically dissimilar locations within Tasmania were acclimated at day/night temperatures of 10/15, 18/23 and 25/30 °C in temperature-controlled greenhouses. Another set of clones was acclimated in a shade-house where temperatures ranged between 10 and 25 °C and with a mean daily temperature of approximately 15 °C. Plants grown at 25/30 °C had significantly lower net photosynthetic rates when measured at 10 and 20 °C than plants grown at lower temperatures. Plants grown at 10/15 °C had significantly lower net photosynthetic rates when measured at 30 °C than plants grown at higher temperatures. Plants grown at the ambient conditions prevailing in midautumn in Hobart had significantly higher net photosynthetic rates at 20 °C than plants raised in the greenhouses and were equal best performers at 10 and 30 °C. A comparison of the light response curves of the plants showed that the maximum rate of net photosynthesis was affected by the growth temperature, whereas the apparent

quantum efficiency remained unchanged. There were no significant differences in the photosynthetic temperature responses of the four genotypes derived from climatically dissimilar locations within Tasmania. A comparison of temperature response models for *E. globulus* indicated that incomplete acclimation (defined by a slope value of less than 1 for the linear relationship between the temperature optimum for photosynthesis and the growth temperature) generally resulted in a greater daily carbon uptake than complete acclimation (slope value of 1).

Keywords: apparent quantum efficiency, genotype, response model, temperature acclimation.

Introduction

Photosynthesis is temperature dependent and exhibits a temperature optimum. In response to small and short-term shifts in ambient temperature away from this optimum, photosynthetic activity decreases; however, it rapidly returns to its previous maximum when the optimum temperature is restored (e.g., Slatyer and Morrow 1977). Longer term deviations from the photosynthetic temperature optimum result in adaptive changes or acclimation in both photosynthesis and respiration (e.g., Mooney and West 1964, Strain et al. 1976, Slatyer and Morrow 1977, Read and Busby 1990). However, in many cases, the slope of the line relating the optimum temperature for photosynthesis and the acclimation temperature is less than 1, but it is often in the range 0.3 to 0.7 (e.g., Billings et al. 1971, Slatyer 1977b, Read 1990), suggesting incomplete acclimation as a result of either the plant's inability to acclimate fully or the plant's ability to regulate the extent of acclimation (Säll and Pettersson 1994). Recently, it has been theoretically demonstrated that incompletely acclimated plants can have higher rates of carbon uptake than fully acclimated plants if the maximum rate of photosynthesis is causally linked with the optimum temperature for photosynthesis (Säll and Pettersson 1994). Detailed studies of seasonal variation in net photosynthesis indicate that this may also be the case in the field (e.g., Slatyer 1977a, 1977b, Slatyer and Ferrar 1977, Slatyer and Morrow 1977), although the optimality of incomplete acclima-

tion remains untested.

We have studied the photosynthetic temperature responses of *Eucalyptus globulus* Labill. subsp. *globulus* and *E. nitens* (Deane and Maiden) Maiden. In southeastern Australia, *E. nitens* is the preferred plantation species in cool environments and *E. globulus* is planted in warm environments. A detailed examination of differences in the photosynthetic temperature responses of the two species may help to identify the environmental factors that cause one species to outperform the other on a particular site. Furthermore, such information is needed for the development of models designed to simulate or predict net carbon accumulation. The specific objectives of this study were to establish the nature of the temperature response curves and the extent to which both species acclimated, and to test whether partial acclimation increased carbon uptake relative to full acclimation. To assess the general applicability of the measured temperature responses, we also examined how the temperature response of photosynthesis in *E. globulus* varied with leaf ontogeny (e.g., Osman and Milthorpe 1971, Jurik et al. 1979) and genotype (e.g., Slatyer 1977b).

Materials and methods

Field measurements

The plantation was established in August 1990 on a rural property 50 km east of Hobart, Tasmania (42°49' S, 147°36' E). The plantation was situated on a fertile basalt soil and was irrigated to maintain the soil water deficit in the top 2 m of the soil profile at between 20 and 40 mm. Fertilizer was applied regularly during stand development. Three adjacent canopies of *E. globulus* trees (seedlot from four families from King Island) and three adjacent canopies of *E. nitens* trees (Forest Resources Seed Orchard stock) were accessed by means of two 10-m tall scaffolds. At each measurement time, an actively growing branch at approximately 90% of tree height on the northern side of the sun canopy was selected. On each branch, the most recently fully expanded leaf from Node 5 (counting down from the apex) was used to monitor monthly changes in photosynthetic temperature response. In December 1993, temperature response curves were determined for *E. globulus* leaves from close to the branch base at approximately Node 20, which arose last growing season, the most recently fully expanded leaf at Node 5, expanding leaves at Node 2, and the apical shoot at Node 0.

Gas exchange measurements

An open gas-exchange system incorporating an infrared gas analyzer (Mk 2, Analytic Development Corp., Hoddesdon, Herts, U.K.) was used to measure net CO₂ and water vapor exchange by foliage. A lamp containing four 150-W Wotan xenon quartz globes was used to maintain an incident photon flux density (PPFD) at the leaf surface of 800 μmol m⁻² s⁻¹. Reductions in irradiance used to derive the light response curves were obtained with neutral-density filters, and increases in irradiance were obtained by increasing the power to the lamp. A humidified air source, consisting of two temperature controlled water baths and an aquarium pump, was used to

maintain the relative humidity close to the leaf surface between 50 and 80%. As a result, the vapor pressure deficit was low for temperatures below 30 °C and unlikely to have significantly affected stomatal conductance. At 30 °C and above, vapor pressure deficits were about 2 kPa, which is sufficient to reduce stomatal conductance by at least 50% (Don White, personal communication). Air at ambient CO₂ concentration was pumped through the leaf chamber (cross-sectional area 6.25 cm²) and the reference line at 400 ml min⁻¹.

Leaf temperature was measured by inserting a thermocouple into the leaf chamber and resting it against the lower leaf surface. Foliage temperature was controlled by circulating water through chambers above and below the leaf chamber. Temperatures were raised in 5 °C steps at approximately 0.5 °C min⁻¹ starting at 10 °C (5 °C in winter) and finishing at 35 °C (40 °C in summer). Leaves were allowed to equilibrate at each measurement temperature for approximately 5 min before each reading was taken. Photosynthetic rates were measured at 15 °C three times, once at the start of the measurement cycle, once under rising temperatures and finally at the end of the measurement cycle under falling temperatures to ensure that no effects of duration of enclosure within the leaf chamber or hysteresis in temperature response were influencing observations.

Conductance of CO₂ from the stomatal cavity to the chloroplast, referred to here as intracellular conductance (g_i), was calculated using the approximation $A/(c_i - \Gamma)$ (Jones 1992), where A is the observed assimilation rate, Γ is the CO₂ compensation point, and c_i is the partial pressure of CO₂ inside the leaf. Within the normal range of leaf temperature, Γ can be approximated as $1.7T$, where T is leaf temperature (Farquhar 1988). The variable c_i was calculated as $(g_c - E/2)(C_c - A)/(g_c + E/2)$, where $1/g_c = 1.6/g_s + 1.37/g_b$, C_c is CO₂ flux corrected for the water vapor pressure in the air, E is the transpiration rate, g_s is the stomatal conductance to water, g_b is the boundary layer conductance, and A is the assimilation rate (von Caemmerer and Farquhar 1981).

Mean hourly readings of air temperature were collected at an automated weather station located in a cleared area adjacent to the plantation. The average of all temperature records for the 5 days preceding the measurement time was used to calculate the growing or acclimation temperature (T_{eff}).

Modeling photosynthetic temperature response

The temperature optimum for each measurement date was calculated from the fit of the equation describing a parabolic temperature response (after Säll and Pettersson 1994):

$$P(T) = P_{\text{opt}} - b(T - T_{\text{opt}})^2, \quad (1)$$

where $P(T)$ is the observed assimilation rate at temperature T , and P_{opt} is the rate of CO₂ uptake at the temperature optimum for photosynthesis, T_{opt} . The parameter b describes the spread of the parabola. The parabolic relationship has been demonstrated to be appropriate for other species of *Eucalyptus* (Slatyer and Morrow 1977); however, the relationship is not universally applicable (see Strain et al. 1976, Pearcy 1978,

Jurik et al. 1988).

The relationship between T_{opt} and the growth temperature, T_{eff} , was defined as (Slatyer 1977c):

$$T_{\text{opt}} = T_{\text{pref}} - \alpha(T_{\text{pref}} - T_{\text{eff}}), \quad (2)$$

where T_{pref} is the temperature at which the optimum temperature for photosynthesis and the growth temperature, T_{eff} , coincide, and α is the acclimation coefficient which describes the linear relationship between T_{opt} and T_{eff} . We have adopted the terminology of Säll and Pettersson (1994) where complete acclimation is equated with an acclimation coefficient of $\alpha = 1$, and hence $T_{\text{opt}} = T_{\text{pref}}$, and incomplete acclimation is equated with an acclimation coefficient of $\alpha < 1$.

It is assumed that b in Equation 1 is independent of T_{opt} but that P_{opt} depends on T_{opt} , and that this dependence can be described by a parabola with a maximum at P_{max} when $T_{\text{opt}} = T_{\text{max}}$ (Säll and Pettersson 1994) as follows:

$$P_{\text{opt}} = P_{\text{max}} - c(T_{\text{opt}} - T_{\text{max}})^2, \quad (3)$$

where c describes the width of the parabola.

Equations 1–3 were combined to give the general equation (equivalent to the stationary model of Säll and Pettersson (1994)):

$$P(T) = P_{\text{max}} - b(T - T_{\text{pref}} - \alpha(T_{\text{pref}} - T_{\text{eff}}))^2 - c(T_{\text{pref}} - \alpha(T_{\text{pref}} - T_{\text{eff}}) - T_{\text{max}})^2. \quad (4)$$

Half-hourly temperature records for the daylight hours for days on which photosynthetic measurements were conducted were used to compare predicted carbon fixation per unit leaf area of leaves assumed to be fully acclimated ($T_{\text{opt}} = T_{\text{eff}}$, cf. Säll and Pettersson 1994) with the photosynthetic response shifts observed in the field. Daylength was varied but light quality was assumed to be uniform, water and nutrition were assumed to be nonlimiting, and no allowance was made for diurnal trends in photosynthetic performance or depression of photosynthesis associated with chilling effects.

Temperature-controlled greenhouse experiments

Sets of *E. globulus* clones were generated from four mother plants from climatically disparate Tasmanian areas: Clone 271 from Leprena, Clones 250 and 312 (known poor and good performers, respectively, at cold sites; Peter Naughton, personal communication), and Clone 310 from Macquarie Harbor. Sets of each clone were acclimated at day/night temperatures of 10/15, 18/23 or 25/30 °C in temperature-controlled greenhouses, and a fourth set of clones was located in a shadehouse providing ambient temperatures that ranged between 10 and 25 °C, with a mean daily temperature for the duration of the experiment of approximately 15 °C. Both the greenhouses and the shadehouse were naturally illuminated throughout the 14-h photoperiod, with a maximum incident PFD inside the greenhouses and shadehouse of approximately 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Clones were raised in 15-cm diameter pots (soil volume of 2650 cm^3) filled with potting mix, watered

three times daily and fertilized with a complete nutrient solution twice a week. After a 3-week acclimation period, plants were shifted to environments providing a constant temperature of 10, 20 or 30 °C and allowed to acclimate for at least 1 h before CO_2 and water vapor exchange measurements were made.

Results

Acclimation responses in the field and response curve fitting

At 20 °C and ambient CO_2 , a photon flux density of 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was saturating, or very nearly so, for both study species (Figure 1). The maximum rate of net assimilation of *E. nitens* was significantly higher than that of *E. globulus*. The initial slope of the light response curve, indicative of the apparent quantum efficiency, was significantly steeper for *E. nitens* than for *E. globulus*.

Examples of photosynthetic temperature response curves for *E. globulus* and *E. nitens* are given in Figures 2 and 3, respectively. The temperature response curves of the two species were generally similar in form; however, the temperature response curves of *E. globulus* showed a more marked temperature optimum than the response curves of *E. nitens*. *Eucalyptus nitens* performed similarly across a 20 to 25 °C range of temperatures, whereas *E. globulus* had a more circumscribed zone of optimum performance encompassing a temperature range between 10 and 15 °C. In *E. nitens*, photosynthesis was only slightly diminished at 10 °C, even in midsummer, whereas *E. globulus* showed a marked decline in photosynthetic performance at temperatures below 15 °C, except during the midwinter acclimation state. As a result, the shape of the photosynthetic temperature response curve was generally parabolic for *E. globulus* but not for *E. nitens*.

The reduction in net photosynthesis at both high and low temperatures was associated with declines in stomatal (g_s) and intracellular conductance (g_i). In general, g_s was not affected by increasing leaf temperature until after g_i and net photosynthesis had commenced to decline. Intracellular CO_2 concentra-

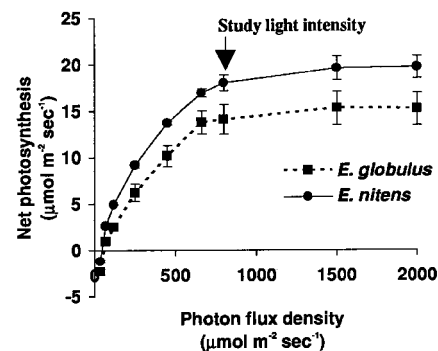


Figure 1. Light response curves of fully expanded leaves from 4-year-old *E. globulus* and *E. nitens* trees assessed on June 21, 1994, at 20 °C, 50% RH and ambient CO_2 (330 ppm). The irradiance during periodic assessment of photosynthetic temperature responses is indicated. Error bars are the 95% confidence interval of the mean.

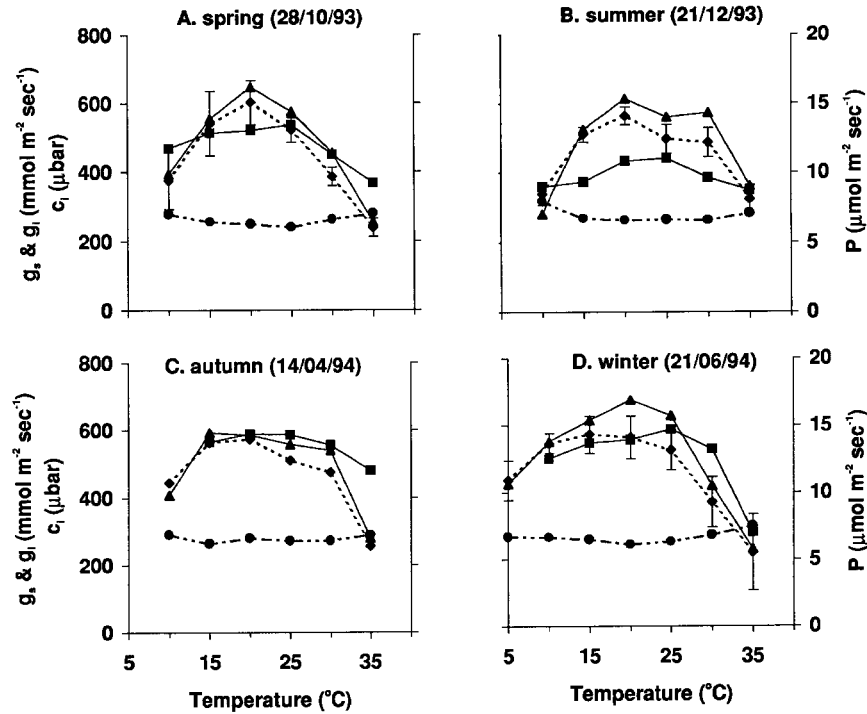


Figure 2. Photosynthetic responses of *E. globulus* to temperature: stomatal conductance (g_s , \blacksquare), intracellular conductance (g_i , \blacktriangle), net photosynthesis (P , \blacklozenge) and intracellular CO_2 (c_i , \bullet). Measurements were made at ambient CO_2 , PAR = $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, and relative humidity close to the leaf surface between 50 and 80%. Error bars are the 95% confidence interval of the mean photosynthetic response.

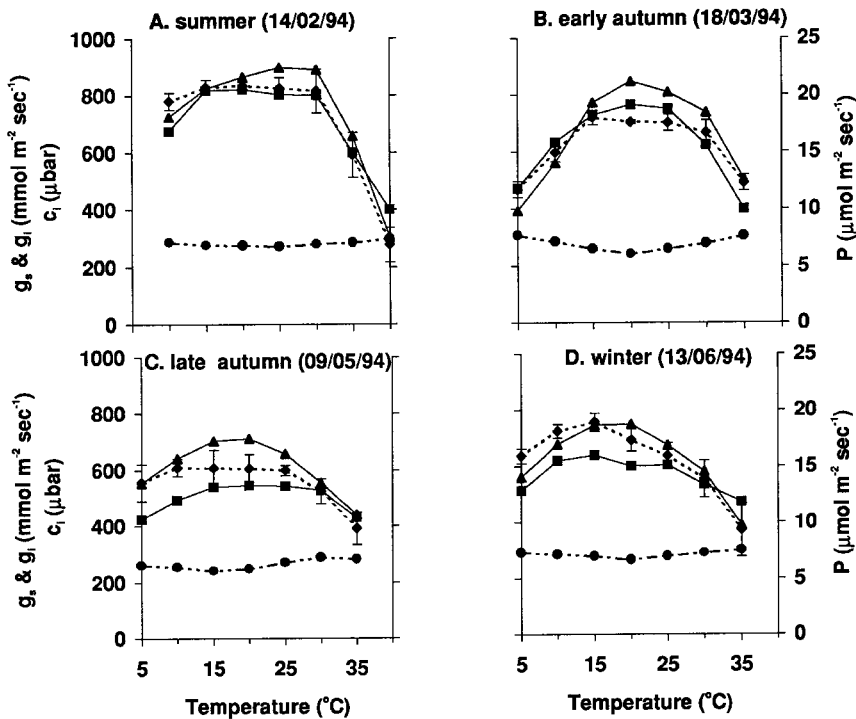


Figure 3. Photosynthetic responses of *E. nitens* to temperature: stomatal conductance (g_s , \blacksquare), intracellular conductance (g_i , \blacktriangle), net photosynthesis (P , \blacklozenge) and intracellular CO_2 (c_i , \bullet). Measurements were made at ambient CO_2 , PAR = $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, and relative humidity close to the leaf surface between 50 and 80%. Error bars are the 95% confidence interval of the mean photosynthetic response.

tions varied within the range of 240–320 μbar (24–32 Pa) for all leaf temperatures tested, being lowest when rates of net photosynthesis were highest. However, the changes in intracellular CO_2 concentrations in response to shifts in leaf temperature were slight compared with the temperature-induced changes in net photosynthesis.

The parameterization of Equation 1, the parabola describing

the relationship between net photosynthesis and measurement temperature, is given in Table 1 for each measurement date. As discussed above, Equation 1 provides a more appropriate description of the temperature response of *E. globulus* than of *E. nitens*, for which the parameter describing the shape of the function, b , is unreliable. In both species, the temperature for maximum photosynthesis, T_{opt} , was linearly related to the

Table 1. Seasonal changes in the shape of the photosynthetic response curve as defined by the parabolic function $P(T) = P_{opt} - b(T - T_{opt})^2$, where P is the rate of photosynthesis at temperature T , with maximum of P_{opt} at temperature T_{opt} , and b describes the spread of the parabola. The average or growth temperature, T_{eff} , is the mean daily temperature of the 5 days preceding the measurement date. Standard errors are given in brackets.

Date	T_{eff} (°C)	P_{opt} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	b	T_{opt} (°C)
<i>E. globulus</i>				
Oct. 28, 1993	12.2	14.4 (0.9)	0.042 (0.009)	20.4 (0.9)
Nov. 25, 1993	12.8	14.2 (0.8)	0.035 (0.009)	20.5 (1.1)
Dec. 21, 1993	15.0	13.8 (0.6)	0.035 (0.006)	22.0 (0.7)
Feb. 8, 1994	16.1	12.6 (0.5)	0.020 (0.005)	23.0 (1.0)
Mar. 8, 1994	11.9	13.7 (0.7)	0.026 (0.005)	19.3 (0.9)
Apr. 14, 1994	8.7	14.4 (1.1)	0.033 (0.011)	19.8 (1.5)
Jun. 21, 1994	6.9	14.1 (1.1)	0.027 (0.008)	16.5 (1.7)
<i>E. nitens</i>				
Feb. 14, 1994	18.9	22.1 (0.7)	0.035 (0.001)	19.9 (1.1)
Mar. 18, 1994	12.5	18.3 (0.4)	0.028 (0.000)	20.7 (0.7)
May 5, 1994	8.6	15.7 (0.5)	0.016 (0.000)	16.8 (1.5)
Jun. 13, 1994	6.8	18.5 (0.6)	0.021 (0.008)	14.1 (1.4)

acclimation temperature, T_{eff} (Figure 4). There was no evidence that the season in which the assessment of photosynthetic performance was made affected the outcome: similar values of T_{eff} in spring and autumn resulted in similar values of T_{opt} .

The optimum temperature for photosynthesis of *E. globulus* increased from 17 to 23 °C with an increase in the mean daily temperature from 7 to 16 °C. Similarly, the optimum temperature for photosynthesis of *E. nitens* increased from 14 to 19 °C when the mean daily temperature was increased from 7 to 19 °C. *Eucalyptus globulus* was more responsive to changes in the temperature of the growing environment than *E. nitens* (α of 0.59 versus 0.35); however, the regression of T_{opt} against T_{eff} for *E. nitens* was heavily influenced by one observation.

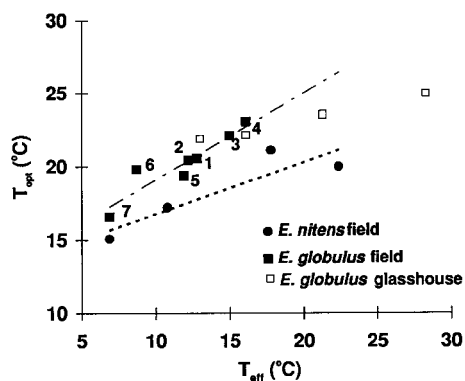


Figure 4. Relationship between the temperature at which maximum photosynthesis was recorded (T_{opt}) and the average temperature of the preceding 5 days (T_{eff}) of both field-grown and greenhouse-grown *E. globulus* and field-grown *E. nitens*. Parameterization follows the equation given by Slatyer (1977c). The equation for field-grown *E. globulus* is $T_{opt} = 32.3 + 0.59(T_{eff} - 32.2)$, $r^2 = 0.86$, $P < 0.05$. The equation for field-grown *E. nitens* is $T_{opt} = 20.4 + 0.35(T_{eff} - 20.4)$, $r^2 = 0.81$, $P < 0.1$. Numbers associated with field-grown *E. globulus* observations indicate the measurement date, where the order follows the list of dates in Table 1.

For *E. globulus*, the relationship between P_{opt} and T_{opt} was described by a parabola (Figure 5, $r^2 = 0.41$, $P < 0.1$) with a P_{max} of $14.35 \mu\text{mol m}^{-2} \text{s}^{-1}$, at a temperature, T_{max} , of 18.9 °C. The three study trees had similar values of T_{max} (19.5, 19.3 and 18.1 °C for Trees 1, 2 and 3, respectively). The P_{max} of Tree 3 was significantly lower than that of the other trees ($13.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ versus 15.1 and $15.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ for Trees 1 and 2, respectively). The relationship of b , the parameter that describes the shape of the parabola, was not correlated with T_{opt} (Figure 6). If Equation 4 is an appropriate description of the acclimation process, then P_{opt} and T_{opt} should be related, and b should be independent of T_{opt} .

Equation 4, which describes the instantaneous net photosynthetic rate in relation to the current temperature and the growing temperature can be parameterized for *E. globulus* as:

$$P(T) = 14.34 - 0.031(T - 32.3 + 0.59(T_{eff} - 32.3))^2 - 0.084(0.59(T_{eff} - 32.3) + 13.4)^2. \quad (5)$$

Equation 5 can be used to assess whether incomplete acclima-

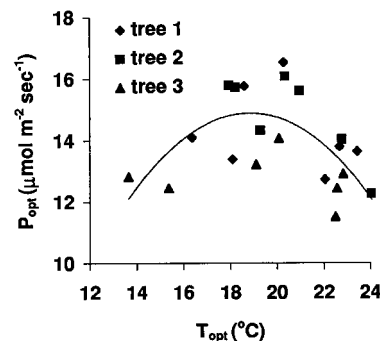


Figure 5. Relationship between the optimum temperature for net photosynthesis (T_{opt}) of *E. globulus* and the maximum rate of photosynthesis observed (P_{opt}).

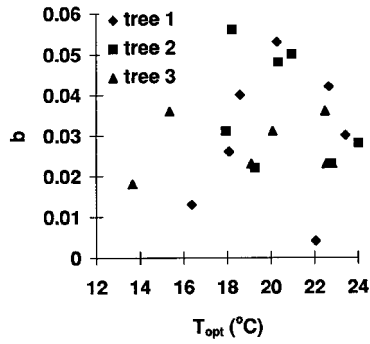


Figure 6. Relationship between the optimum temperature for net photosynthesis (T_{opt}) of *E. globulus* and b , a parameter that describes the width of the parabolic temperature response curve.

tion represents an inability of a plant to optimize its response. In the case of complete acclimation (*sensu* Säll and Petterson 1994), T_{opt} would equal T_{eff} and Equation 5 would become:

$$P(T) = 14.35 - 0.031(T - T_{eff})^2 - 0.084(T_{eff} - 18.9)^2. \quad (6)$$

It is not known whether P_{opt} is causally determined by T_{opt} , as Säll and Petterson (1994) imply, or casually correlated with T_{opt} as a result of seasonal correlations between injury and acclimation. In the case where P_{opt} remains constant and T_{opt} shifts (e.g., Sands 1996), Equation 5 becomes:

$$P(T) = 14.35 - 0.031(T - T_{eff})^2 - 0.084(0.59(T_{eff} - 32.3) + 13.4)^2. \quad (7)$$

Using the average hourly temperature for the week before measurement, the carbon uptake of *E. globulus* leaves can be estimated from Equations 5–7, assuming that temperature is the only limiting factor (Table 2). In all but one case, the model for the incomplete acclimation state predicted greater productivity for the measurement dates than did the model for the fully acclimated state. However, the model for the fully acclimated state with P_{opt} held constant predicted the greatest productivity in all but two cases, although the difference was only slight for one case.

Table 2. Estimated productivity of trees allowing for incomplete and complete acclimation where the maximum rate of photosynthesis (P_{opt}) is causally related to the optimum temperature for photosynthesis (T_{opt}) (Equations 5 and 6), and full acclimation where T_{opt} and P_{opt} are independently determined (Equation 7).

Date	Weekly average T_{eff} (°C)	Estimated daily CO ₂ uptake (mol CO ₂ m ⁻²)		
		Incomplete acclimation (Equation 5)	Full acclimation (Equation 6)	Full acclimation (Equation 7)
Oct. 28, 1993	12.2	608	475	642
Nov. 25, 1994	12.8	650	601	753
Dec. 21, 1994	15.0	583	576	590
Feb. 8, 1994	16.1	680	705	673
Mar. 8, 1994	11.9	574	474	659
Apr. 14, 1994	8.7	542	169	514
Jun. 21, 1994	6.9	334	69	454

Leaf age effects

Leaves of different ages exhibited different photosynthetic responses to temperature (Figure 7). In December 1993, apical shoots, expanding leaves, fully expanded leaves from current-year growth, and fully expanded leaves from the previous-year's growth had photosynthetic temperature optima of 10–15, 15, 20 and 20–25 °C, respectively.

Greenhouse experiments with different genotypes of *E. globulus*

Greenhouse-grown plants acclimated to the growth environment in the same way as field-grown plants, although changes in the photosynthetic temperature optima were slight compared to the shifts detected in the field (Table 3, Figure 8). The field and greenhouse data were generally similar at T_{eff} values below 20 °C, but plants grown at > 20 °C in the greenhouse showed a less marked shift in T_{opt} than predicted from older field-grown plants (Figure 4), perhaps indicating a limit to the acclimation ability of *E. globulus* or a fundamental difference between field-grown trees and greenhouse-grown plants in the

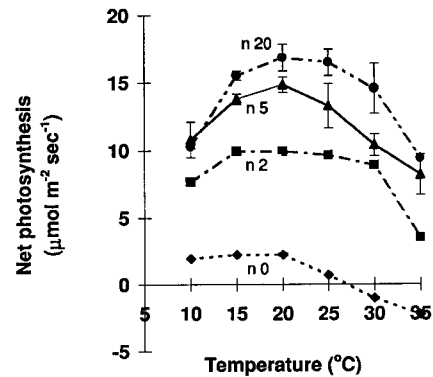


Figure 7. Photosynthetic temperature response curves of leaves of *E. globulus* along a branch measured on December 21, 1993. Apical shoot = n 0; 2nd node counting back from the apex = n 2; 5th node from the apex = n 5; and 20th node from the apex = n 20. Measurements were made at ambient CO₂, PAR = 800 µmol m⁻² s⁻¹, and relative humidity close to the leaf surface between 50 and 80%. Error bars are the 95% confidence interval of the mean.

Table 3. Analysis of variance for the interaction of acclimation temperature (ACCT), genotype (GENO) and measurement temperature (TEMP) on net photosynthesis after allowing for between subject (PLANTNO) differences.

Source	DF	Type III SS	Mean square	F-value	P
PLANTNO (ACCT × GENO)	66	422.1	6.4	1.81	0.0037
ACCT × GENO	8	12.3	1.5	0.44	0.8963
TEMP	2	1805.4	902.7	255.18	0.0001
TEMP × GENO	6	12.7	2.1	0.60	0.7297
TEMP × ACCT	6	109.9	18.3	5.18	0.0001
TEMP × ACCT × GENO	16	27.4	1.7	0.49	0.9489
<i>Tests of hypotheses using the Type III MS for PLANTNO(ACCT × GENO) as an error term</i>					
GENO	3	17.9	6.0	0.93	0.4296
ACCT	3	212.9	71.0	11.10	0.0001

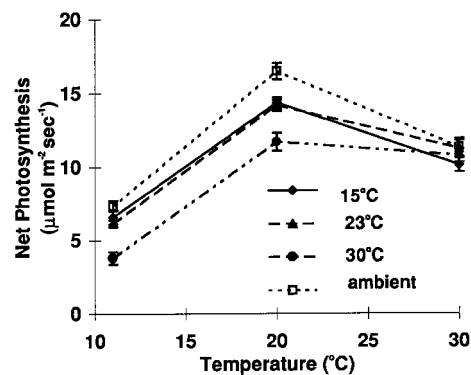


Figure 8. Photosynthetic rates at 10, 20 and 30 °C of *E. globulus* acclimated for 3 weeks at 15/10, 18/23 or 25/30 °C in greenhouses or in a shadehouse at ambient temperature. Error bars are the 95% confidence interval of the mean.

slope ($\alpha = 0.12$ for the greenhouse-grown plants) of the line relating acclimation temperature to T_{opt} .

Plants acclimated at 30 °C in the greenhouse had significantly lower rates of CO₂ uptake at 10 and 20 °C than did plants acclimated at 15 and 23 °C, but performed equally well when tested at 30 °C. Plants raised in a 15 °C greenhouse had similar rates of CO₂ uptake to plants raised in a 23 °C greenhouse when tested at 10 and 20 °C but had a significantly ($P < 0.05$) lower rate of CO₂ uptake when tested at 30 °C. Plants acclimated under varying temperature conditions in the shadehouse performed significantly better than all other plants when tested at 20 °C. Plants grown in the shadehouse had a T_{opt} of 21.8 °C, and plants grown in the 10/15, 18/23 and 25/30 °C greenhouses had T_{opt} values of 21.8, 22.6 and 24.1 °C, respectively. Plants grown in the 10/15, 18/23 and 25/30 °C greenhouses had P_{opt} values of 14.56, 14.58 and 12.65 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Applying Equation 4 to the greenhouse-grown plants yielded best-fit values of $T_{max} = 21.82$ and $P_{max} = 14.77$, values that are similar to those of the field-grown plants. The effect of measurement temperature on instantaneous net photosynthesis was also similar for the field- and greenhouse-grown plants ($b = 0.031$ for the field-grown plants compared with 0.047 for greenhouse-grown plants) but the change in P_{opt} with T_{opt} was

considerably less for the field-grown plants ($c = 1.54$ for greenhouse-grown plants compared with 0.084 for field-grown plants).

The apparent quantum efficiency was independent of the growth temperature (Figure 9). Clones of all four genotypes performed similarly under all test conditions, both in terms of overall photosynthetic performance and in shifts in photosynthetic response as a result of changes in growth temperature (Table 3).

Discussion

The photosynthetic temperature response curves of mature leaves of *E. globulus* were generally parabolic and symmetrical around the temperature optimum (cf. Säll and Pettersson 1994), whereas the photosynthetic temperature response of *E. nitens* was not satisfactorily described by the parabolic function. The skewed response to temperature observed in some species (e.g., Strain et al. 1976, Pearcy 1978, Jurik et al. 1988) and the platykurtic response of *E. nitens* observed in this study indicate that the parabolic function is not universally applicable.

The decline in net photosynthesis above and below the temperature optimum was accompanied by declines in both

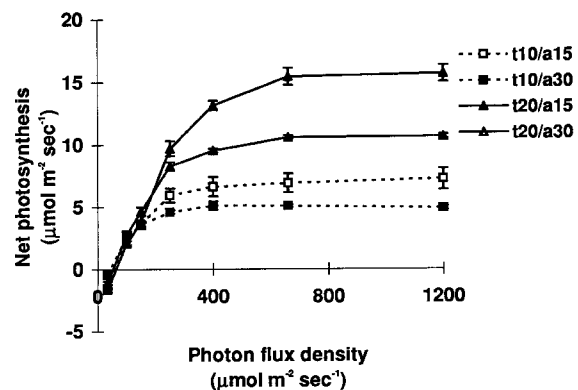


Figure 9. Light response curves of *E. globulus* acclimated at 15/10 (a15) or 25/30 °C (a30) in greenhouses and measured at 10 (t10) or 20 °C (t20). Error bars are the 95% confidence interval of the mean.

stomatal conductance and intracellular conductance. However, the decline in net photosynthesis commenced before the decline in stomatal conductance, suggesting that the initial changes in net photosynthesis are a result of decreased intracellular conductance. At temperatures above 25 °C, when net photosynthesis had already commenced to decline, the atmospheric vapor pressure deficit was almost certainly a factor in the reduction in stomatal conductance.

Leaf age was an important determinant of the shape of the photosynthetic response curve. Older leaves of *E. globulus* had a higher photosynthetic temperature optimum and a more symmetrical photosynthetic temperature response curve than older leaves of *E. nitens*. These differences are likely to be the result of different rates of growth respiration rather than differences in acclimation of the photosynthetic apparatus, because the increase in respiration rate with increasing temperature is generally greater than the increase in carboxylation rate (Berry and Björkman 1980). Normally, young tissues have higher respiration rates than older tissues, and developing tissues have higher respiration rates than mature tissues (Bidwell 1979). This explains both the decrease in photosynthetic optima and the increase in asymmetry of the temperature response curve as progressively younger and more actively growing leaves were examined.

The photosynthetic temperature response curve of *E. nitens* was broader than that of *E. globulus*. Broad photosynthetic temperature response curves are often found in species, or ecotypes of species, from variable environments (e.g., Billings et al. 1971, Read 1990). *Eucalyptus nitens* occurs in environments ranging in altitude from 600 to 1600 m that are prone to frosts, in which the coldest month of the year has a mean minimum temperature of -5 to 2 °C and the warmest month has a mean maximum temperature of 21 to 26 °C. In contrast, *E. globulus* subsp. *globulus* is typically found within 20 km of the coast at altitudes ranging between sea-level and 450 m, where the mean minimum temperature of the coldest month varies between 0 and 8 °C and the mean maximum temperature of the warmest month varies between 20 and 23 °C (Boland et al. 1984). More importantly, the more continental climate prevalent across the environmental range of *E. nitens* results in a greater diurnal range of temperatures. Although acclimation to broad seasonal shifts in temperature is important for *E. nitens*, a broad photosynthetic temperature optimum also has the advantage that it greatly increases potential CO₂ uptake. Thus, Turnbull et al. (1993) found that the productivity of *E. nitens* changed only slightly over a 600 m altitudinal range, whereas the productivity of *E. globulus* exhibited a pronounced optimum at the lower altitude sites, but only when these sites were frost free.

We conclude that both *E. globulus* and *E. nitens* are capable of acclimation. Changes in photosynthetic performance in response to temperature were detected that appeared to be independent of intracellular CO₂ concentration. The relationship between growth environment and optimum temperature for photosynthesis was linearly correlated for both species (cf. Slatyer 1977b). Greenhouse experiments indicated that at very high growth temperatures (average daily temperature of

28 °C), the extent of acclimation may be diminished, although the possibility that the greenhouse-grown plants followed a different acclimation trajectory than the older field-grown trees cannot be discounted. Comparable temperatures in spring and autumn resulted in similar optimum temperatures for net photosynthesis, indicating no significant hysteresis in the acclimation response. Based on this finding, we conclude that shifts in the photosynthetic temperature optimum are a direct response to growth temperature.

The data suggest that *E. globulus* acclimates more completely than *E. nitens* ($\alpha = 0.59$ versus 0.35). This may be because the broader photosynthetic temperature response curve of *E. nitens* necessitates a less dynamic response to changing temperature. *Eucalyptus globulus*, which grows in an environment characterized by less diurnal temperature fluctuations than *E. nitens*, has a narrowly defined zone over which net photosynthesis remains at near maximal rates, but a fairly dynamic response to growth temperature. By contrast, the photosynthetic response of *E. nitens* is not closely tied to changes in growth temperature. The adverse effects of this pattern of response are probably counterbalanced by the broad temperature optimum for photosynthesis which enables high rates of photosynthesis to be maintained over a wide diurnal temperature range.

In both species, acclimation was only partial, defined by a value of less than 1 for the slope of the line relating the optimum temperature for photosynthesis to the growth temperature. Although the maximum rate of photosynthesis changed only slightly over the 9-month measurement period, the changes were sufficient to support the contention of Säll and Petterson (1994) that incomplete acclimation could result in greater carbon uptake if the maximum rate of photosynthesis and the temperature optimum of photosynthesis are causally linked. However, this contention is not substantiated if the maximum rate of photosynthesis is only coincidentally correlated with the temperature optimum of photosynthesis and acclimation changes to the temperature optimum for photosynthesis do not necessitate a change to the seasonally determined maximum rate of photosynthesis. Although seasonal effects on net photosynthesis have been associated with winter injury (e.g., Slatyer and Morrow 1977, Linder and Lohammar 1981) or midsummer high temperature injury (e.g., Mooney et al. 1978) in extreme environments, it is unlikely that these effects are important at the field site used in this study. It is not known whether the decline in maximum rate of net photosynthesis observed in plants grown in the greenhouse at high temperatures and the decline and recovery associated with the onset and passing of summer reflect injury or an acclimation associated linkage. In addition to the possible optimality of incomplete acclimation for CO₂, factors such as the high metabolic costs associated with low temperature acclimation and the associated marginal photosynthetic gain (Berry and Björkman 1980) indicate that interpretation of adaptive fitness from acclimation response alone is simplistic.

Eucalyptus globulus ramets raised from four parent plants from geographically different locations showed similar photosynthetic temperature responses even though at least two of the

clones differed in growth response to site temperature in field trials (Peter Naughton, personal communication). This finding suggests that the photosynthetic temperature response is a conservative trait in *E. globulus*, in contrast to other species (e.g., Billings et al. 1971, Slatyer and Morrow 1977, Slatyer 1977b, Turnbull et al. 1993). However, the differences among the genotypes observed in field trials may be related to differences in frost resistance rather than photosynthetic differences (Turnbull et al. 1993). The four genotypes were selected from sites that might be regarded *a priori* as differing significantly in temperature environment. It is possible that the generally maritime nature of the *E. globulus* subsp. *globulus* geographic range and its restricted latitudinal distribution have resulted in a low between-site variability in temperature environment and thereby prevented the development of ecotypic differences in photosynthetic temperature response that are observed among species with a greater latitudinal or altitudinal distribution.

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