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S.C. Cunningham · J. Read

Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature

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Abstract Little is known about the differences in physiology between temperate and tropical trees. Australian rainforests extend from tropical climates in the north to temperate climates in the south over a span of 33° latitude. Therefore, they provide an opportunity to investigate differences in the physiology of temperate and tropical trees within the same vegetation type. This study investigated how the response of net photosynthesis to growth temperature differed between Australian temperate and tropical rainforest trees and how this correlated with differences in their climates. The temperate species showed their maximum rate of net photosynthesis at lower growth temperatures than the tropical species. However, the temperate species showed at least 80% of maximum net photosynthesis over a 12–16°C span of growth temperature, compared with a span of 9–11°C shown by the tropical species. The tropical species showed both larger reductions in maximum net photosynthesis at low growth temperatures and larger reductions in the optimum instantaneous temperature for net photosynthesis with decreasing growth temperature than the temperate species. The ability of the temperate species to maintain maximum net photosynthesis over a greater span of growth temperatures than the tropical species is consistent with the greater seasonal and day-to-day variation in temperature of the temperate climate compared with the tropical climate.

Keywords Climate · Latitude · Maximum net photosynthesis · Optimum temperature · Photosynthetic plasticity

S.C. Cunningham (✉) · J. Read
School of Biological Sciences, Monash University,
Melbourne, Victoria 3800, Australia
e-mail: shaun.cunningham@sci.monash.edu.au
Tel.: +61-03-99055622, Fax: +61-03-99055613

Present address:
S.C. Cunningham, 4 Hakea Crescent, O'Connor, ACT 2602, Australia

Introduction

Differences between tropical and temperate forests have long interested ecologists. Much research has focused on explanations for the maintenance of the considerably higher diversity in tropical forests than temperate forests (e.g. Connell 1978; Grubb 1977; Hubbell and Foster 1986). There has been little research, particularly direct comparisons, into physiological differences between tropical and temperate species. The few studies that compare tropical and temperate species are often complicated by comparisons of different growth forms (e.g. Franks and Farquhar 1999; Schreiber and Riederer 1996).

The predominant changes in climate from temperate to tropical forests are the increase in temperature and the reduction in seasonality of temperatures (Archibold 1995). These climate differences are reflected in the phenology of these forests, with growth cycles in temperate forests generally associated with temperature, whereas growth cycles in tropical forests tend to be associated with precipitation (Lechowicz 1995; Reich 1995). Consequently, research on the physiology of tropical trees in relation to climate has often concentrated on water relations (e.g. Fetcher et al. 1994; Medina 1983; Mulkey et al. 1996; Robichaux et al. 1984). Considering temperature is one of the primary differences between tropical and temperate climates, it is important to gain an understanding of the difference between the responses of temperate and tropical species to temperature. A knowledge of these differences will improve our understanding of the effects of predicted global increases in temperature on tree distribution.

Rainforests occur across a latitudinal range of 33° in Australia, which includes climates from cool-temperate to tropical. These forests have a disjunct distribution along the eastern margin of Australia, being restricted to areas that have a high annual rainfall (>1,300 mm) and low fire frequency (Specht and Specht 1999; Webb and Tracey 1994). Therefore, they provide an opportunity to study the temperature responses of temperate and tropical species within the same mesic forest type.

Recent work with Australian rainforest trees has shown differences in photosynthetic responses among species from different latitudes. A study of temperate rainforest trees found that species from lower latitudes showed maximum photosynthesis at higher temperatures than species from higher latitudes (Hill et al. 1988). In contrast, tropical and temperate species of *Nothofagus* showed little difference in the temperature for maximum photosynthesis (Read 1990). Instead, the difference was the ability of temperate species to acclimate to a wider range of temperatures than tropical species. This is consistent with the tropical species of *Nothofagus* being from high altitudes areas with similar summer temperatures to temperate climates but with less seasonal variation in temperature. These previous studies measured the acclimation potential of species, which is a measure of the ability of mature leaves to adjust their photosynthetic response to new temperatures. The photosynthetic responses reported in these studies may not reflect the full photosynthetic potential of the tropical species as leaves were developed at moderate temperatures.

The term photosynthetic *acclimation* is often loosely used in the literature to describe all changes in photosynthesis in response to temperature (e.g. Berry and Björkman 1980; Öquist 1983). However, young, developing leaves are able to make greater adjustments in response to temperature changes than mature, fully expanded leaves (Falk et al. 1996). Therefore, throughout this paper, we will refer to differences between leaves initiated and developed under different growth temperatures as *photosynthetic plasticity* and changes in mature leaves induced by altered growth temperatures as *photosynthetic acclimation*.

The present work investigated differences in the plasticity of the photosynthetic response to temperature and tropical trees. In particular, it aimed to determine if the differences in acclimation responses to temperature previously found among rainforest species are true of photosynthetic plasticity in a broader range of rainforest genera. That is:

1. Do temperate species show maximum net photosynthesis at lower growth temperatures than tropical species?
2. Do temperate species show close to maximum net photosynthesis over a greater span of growth temperatures than tropical species?

These questions were tested using eight rainforest species native to different latitudes and by comparing the photosynthetic capacity of leaves developed under five growth temperature regimes.

Materials and methods

Species selection

Eight species were selected to represent the wide range of climates in which rainforests grow in eastern Australia. Two species were selected from each of the four rainforest types (cool-temperate, warm-temperate, subtropical and tropical) defined by Webb (1968). Canopy species were used as previous research has shown that subcanopy species can have narrower photosynthetic responses to temperature than would be predicted from their macroclimate distribution (Read and Busby 1990). All species were evergreen, ensuring that their leaves are exposed to the full seasonal changes of temperature. Species that occur in lowland rainforest were selected to avoid tropical species restricted to the cooler climates of tropical mountains. Species from different families were chosen where possible to minimise the confounding effects of phylogenetic relatedness. The species, collection sites and distributional ranges are shown in Table 1.

Climate analysis

An extensive collection of site locations (latitude, longitude and altitude) was made for each of the study species from herbariums, forestry departments and seed suppliers in Australia. The ANUCLIM 5.0 program (Houlder et al. 1999) was used to determine climate profiles of these site locations. These values were then used to determine the mean climate profiles for the species.

Growth conditions

All species were collected as seedlings from natural populations except for the two tropical species *Alstonia scholaris* and *Castanospermum australe*, which were raised from seed collected from natural populations. Seedlings were grown in sandy loam soil in glasshouses for a year prior to the experiment. Seedlings were watered every 2 days and fertiliser was added every 14 days in the

Table 1 The species used in the study, grouped into climate types and with details of their collection sites and distributional ranges

	Collection site			Distributional range	
	Latitude	Longitude	Altitude (m)	Latitude	Altitude (m)
Temperate species					
Eucryphia lucida (Labill.) Baill. (Eucryphiaceae)	41°10′S	144°57′E	140	41–43.5°S	5–1,000
Nothofagus cunninghamii (Hook.) Oerst. (Fagaceae)	41°09′S	145°01′E	180	37–43.5°S	0–1,440
Tristaniopsis laurina (Sm.) Wilson & Waterhouse (Myrtaceae)	37°42′S	147°22′E	150	25.5–38°S	5–1,035
Acmena smithii var. *smithii* (Poir.) Merrill & Perry (Myrtaceae)	37°25′S	149°49′E	200	24.5–39°S	0–1,270
Tropical species					
Sloanea woollsii F. Muell. (Elaeocarpaceae)	30°43′S	152°43′E	60	26–32°S	20–1,200
Heritiera trifoliolata (F. Muell.) Kosterm. (Sterculiaceae)	28°36′S	152°43′E	540	17–30°S	10–1,075
Castanospermum australe Cunn. & C. Fraser ex Hook. (Fabaceae)	26°38′S	153°38′E	40	12.5–30°S	5–1,150
Alstonia scholaris (L.) R. Br. (Apocynaceae)	16°13′S	145°52′E	20	10.5–22°S	0–1,300

form of FOGG-IT fish emulsion fertilizer (FOGG-IT Nozzle Company, San Francisco) diluted 1/500 with water to provide 98 mg l^{-1} of nitrogen, 20 mg l^{-1} of potassium, and 31 mg l^{-1} of phosphorus. At the beginning of the experiment, seedlings of *C. australe* were too large to fit in the controlled-environment cabinets, so 1-month-old seedlings were used.

Seedlings of the eight species were grown in five controlled-environment cabinets (TRENT Refrigeration, Melbourne) each with a different day/night temperature regime (16 h photoperiod). The regimes were 14°C/6°C, 19°C/11°C, 22°C/14°C, 25°C/17°C and 30°C/22°C. The two extreme temperature regimes were chosen to cover the widest range of sublethal temperatures for all species and the intermediate temperatures were chosen to span the temperature range over which maximum net photosynthesis was believed to occur. Light (PPFD) was supplied by four 1,000 W metal halide lamps and levels at the tops of seedlings ranged from 600–800 µmol m^{-2} s^{-1} within each cabinet, which is above the light-saturation point for photosynthesis for all species (Cunningham 2001). Vapour pressure deficit during the daytime ranged from 1.06±0.03 kPa in the 14°C/6°C cabinets to 2.12±0.08 kPa in the 30°C/22°C cabinets. The CO_2 concentration inside the cabinets ranged between 345 and 370 µl l^{-1}. The experiment was performed in two separate runs between May and November 1997, allowing each temperature treatment to be housed in two different cabinets. Five plants of each species were grown in each cabinet, with the exception of *C. australe* for which six plants were grown in each cabinet in the second run only.

Photosynthetic measurements were recorded from the most recent leaves to fully expand under the experimental treatments. For each species, three seedlings were measured from each growth temperature regime during both runs of the experiment, i.e. six plants per treatment. However, for *C. australe*, measurements were taken from six seedlings grown in the second run of the experiment. The optimum temperatures for net photosynthesis (T_{opt}) and the net photosynthetic rates at the optimum temperatures (P_{max}) were determined from plants grown under the five temperature regimes. Instantaneous temperature dependence (ITD) curves were determined for the seedlings from the 14°C/6°C, 22°C/14°C and 30°C/22°C temperature regimes.

Photosynthesis was measured using an ADC LCA4 infrared gas analyser (ADC, UK), which is an open gas-exchange system. The leaf was equilibrated at an air temperature of 22±0.1°C, a CO_2 concentration of 350±5 µl l^{-1}, a vapour pressure deficit of 1.05±0.05 kPa and a PPFD of 800±20 µmol quanta m^{-2} s^{-1} until a steady rate was reached. For the ITD curves, measurements were taken at 10°C, 14°C, 18°C, 20°C, 22°C, 24°C, 26°C, and 30°C. The VPD was maintained at a constant 1.05 kPa at all air temperatures and the leaf was allowed to equilibrate for 5 min at each new temperature before measurement. For the seedlings from the 19°C/11°C and 25°C/17°C cabinets, P_{max} and T_{opt} were measured by changing the air temperature in 1°C intervals until a distinct maximum was shown. The area of leaf within the gas chamber was traced and the traces were measured using image analysis (Bioscan Image Analyser).

Data analysis

The ITD curves tended to be asymmetrical, with the rate dropping off more rapidly at higher temperatures. Therefore, quadratic equations used by other researchers (e.g. Sall and Pettersson 1994) did not provide an accurate fit. The following regression curve was found to be appropriate (Ratkowsky et al. 1983):

$$P = \{b(T - T_{min}) \times [1 - \exp(e(T - T_{max}))]\} \quad (1)$$

where P is the net photosynthetic rate (µmol m^{-2} s^{-1}), T is the air temperature (°K), T_{min} and T_{max} are the minimum and maximum temperatures at which the net photosynthetic rate is zero, and b and c are fitting parameters. T_{min} and T_{max} were simply parameters estimated to fit the curve and their values were believed to have no physiological significance. These regression curves were used to estimate P_{max}, T_{opt}, and the temperature span over which at least 80% of P_{max} was shown (T_{span}) of leaves grown under the 14°C/6°C, 22°C/14°C and 30°C/22°C temperature regimes.

The overall experiment was a split-plot design with the five controlled-environment cabinets from the two runs treated as ten separate plots, growth temperature as the effect between cabinets and species as the effect within cabinets. Data were first analysed grouped by species using the averaged values of the three subreplicate plants of a species in each cabinet. Then the data were analysed grouped into two climate groups: temperate (*Acmena smithii*, *Eucryphia lucida*, *Nothofagus cunninghamii* and *Tristaniopsis laurina*) and tropical (*Alstonia scholaris*, *Castanospermum australe*, *Heritiera trifoliolata* and *Sloanea woollsii*). Because the same four species were used in both runs, species within cabinets of the same temperature were not true replicates of the climate groups. To include the variation in responses of the individual species, the climate groups were analysed as a one-way ANOVA using species means.

For each species, the mean values of P_{max} for each growth temperature regime were regressed against growth temperature separately for each run using Eq. 1. The maximum rates of P_{max} (P_{GTmax}), the optimum growth temperatures for P_{max} (GT_{opt}) and the span of temperatures over which at least 80% of P_{GTmax} was shown (GT_{span}) were determined from these regressions. For individual species, these parameters were analysed as a randomised complete block design, with run as the blocking variable. For the climatic groups, the mean values of the parameters for each species were regressed using Eq. 1 and one-way ANOVA used to analyse the derived parameters. A Bonferroni adjustment was used on probability values for all pairwise comparisons of means. A critical value of α=0.05 was used for all tests of significance.

Results

Climate analysis

The results of the climate analysis are shown in Table 2. The magnitude of mean and maximum temperatures experienced by each species decreased with increasing latitudinal origin of the species. In contrast, the temperate species generally experience a greater annual range of maximum temperatures than the tropical species but have a similar diurnal temperature range.

Effect of growth temperature on maximum net photosynthesis

The maximum rate of net photosynthesis (P_{max}) changed with growth temperature for all species (Fig. 1). The highest values of net photosynthesis shown by a species ranged from 3.3 µmol m^{-2} s^{-1} for *Castanospermum australe* to 10.8 µmol m^{-2} s^{-1} for *Tristaniopsis laurina* (Table 3). The low rate of net photosynthesis in *C. australe* is consistent with its known shade tolerance (Osmond 1987). There was no significant difference between the highest values of net photosynthesis shown by the climate groups (F=0.25, P=0.64). The percentage difference between the highest and lowest values of P_{max} shown across the five growth temperatures was 34% for temperate species and 62% for tropical species.

The optimum growth temperatures for maximum net photosynthesis (GT_{opt}) ranged from 18.7°C to 27.3°C among the species (Table 3). GT_{opt} increased with de-

Table 2 Climate profiles for the study species. Values are means of n site locations, with standard errors in parentheses, of the climate profiles produced by ANUCLIM 5.0 for individual site locations. Species are presented in order from highest to lowest latitudinal origin

	Mean annual temperature (°C)	Maximum temperature hottest quarter (°C)	Maximum temperature coldest month (°C)	Maximum temperature range (°C)	Max. temperature range hottest 6 months (°C)	Mean diurnal range (°C)	Mean annual precipitation (mm)
E. lucida (*n*=112)	9.3 (0.1)	18.0 (0.1)	8.7 (0.2)	10.2 (0.1)	6.0 (0.1)	8.6 (0.1)	2,072 (52)
N. cunninghamii (*n*=354)	9.2 (0.1)	18.7 (0.1)	7.8 (0.1)	11.7 (0.1)	6.4 (0.1)	8.6 (0.1)	1,764 (28)
T. laurina (*n*=137)	16.2 (0.2)	26.1 (0.2)	16.3 (0.2)	10.2 (0.1)	4.0 (0.1)	11.2 (0.2)	1,318 (34)
A. smithii (*n*=291)	16.4 (0.1)	26.1 (0.1)	16.0 (0.2)	10.5 (0.1)	4.2 (0.1)	10.7 (0.2)	1,320 (24)
S. woollsii (*n*=140)	15.8 (0.2)	26.0 (0.1)	15.9 (0.2)	10.6 (0.1)	3.8 (0.0)	11.6 (0.2)	1,395 (27)
H. trifoliolata (*n*=98)	18.3 (0.2)	27.3 (0.2)	18.6 (0.2)	9.1 (0.1)	3.2 (0.1)	10.7 (0.2)	1,750 (64)
C. australe (*n*=123)	20.7 (0.2)	29.0 (0.2)	21.4 (0.3)	8.1 (0.1)	2.8 (0.1)	10.4 (0.3)	1,655 (59)
A. scholaris (*n*=61)	23.0 (0.3)	30.2 (0.2)	23.5 (0.3)	7.1 (0.2)	2.3 (0.1)	9.0 (0.3)	1,978 (94)

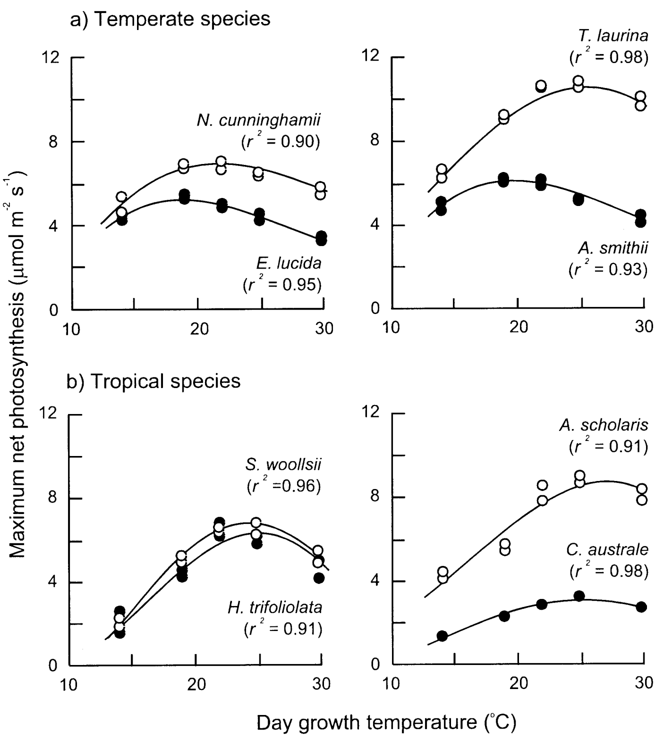

Fig. 1 Relationship between maximum net photosynthesis and day growth temperature for the individual species. Values of P_{max} are means of each run with *C. australe* only measured in one run

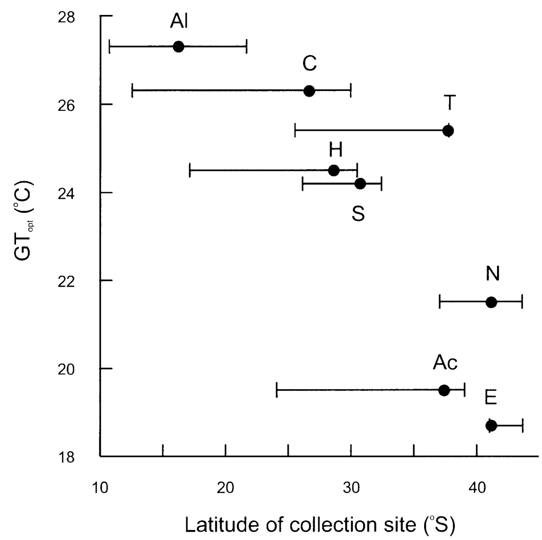

Fig. 2 Relationship between the day growth temperature for maximum net photosynthesis (GT_{opt}) and the latitudinal range of the species. The species are labelled as follows: *Acmena smithii* (typical form) (*Ac*), *Alstonia scholaris* (*Al*), *Castanospermum australe* (*C*), *Eucryphia lucida* (*E*), *Heritiera trifoliolata* (*H*), *Nothofagus cunninghamii* (*N*), *Sloanea woollsii* (*S*) and *Tristaniopsis laurina* (*T*). For each species, the *dot* marks the collection site and the *bars* represent the distributional range

creasing latitudinal origin of the species with the exception of the temperate species *Acmena smithii* (Fig. 2). *Acmena smithii* showed a GT_{opt} of 19.5°C, which is low considering its distribution extends well into tropical climates. The GT_{opt} for the tropical group at 25.6±0.7°C was significantly higher than the GT_{opt} for the temperate group at 21.3±1.5°C (F=6.85, P=0.04).

The temperate species showed at least 80% of P_{GTmax} over greater spans of growth temperature (12–16°C) than the tropical species (9–11°C; Table 3). The only statistically significant difference among species was the greater span of *Nothofagus cunninghamii* compared to that of *Alstonia scholaris*. However, the temperate group showed at least 80% of P_{GTmax} over a significantly larger span of growth temperatures (14.1±0.9) than the tropical group (9.5±0.4, F=21.8, P<0.01).

Effect of growth temperature on the optimum temperature for net photosynthesis

All species, except *Eucryphia lucida*, showed a linear increase in the optimum temperature for net photosynthesis (T_{opt}) with increasing growth temperature (Table 4). The increase in T_{opt} with a 1°C increase in day growth temperature varied among species, ranging from 0.1°C/°C in the temperate species *T. laurina* to 0.5°C/°C in the tropical species *A. scholaris*. T_{opt} of the tropical group increased from 21°C to 26°C between the day growth temperatures of 14°C and 30°C whereas the temperate group only increased from 20°C to 23°C. This resulted in the tropical group having a significantly higher T_{opt} than the temperate group when grown under the temperature regimes of 22°C/14°C and 25°C/17°C (Table 5).

Effect of growth temperature on the span of the photosynthetic response to instantaneous temperature

For each species the temperature span over which at least 80% of P_{max} was achieved did not change significantly with growth temperature (F=1.04, P=0.37). The tropical species *C. australe* showed a reduced temperature span of 14°C when grown at 30°C/22°C compared with a span of 16°C at the other growth temperatures. However, this could not be statistically tested as this species was only grown in one run of the experiment. Species only showed significant differences in the temperature span over which at least 80% of P_{max} was achieved when grown at 14°C/6°C (Table 6). However, trends among species were not consistent between runs. The temperature span for 80% of P_{max} of the climate groups did not change significantly with growth temperature (F=0.24, P=0.80).

Effect of growth temperature on net photosynthesis at extreme temperatures

Species showed significant changes with growth temperature in the percentage of P_{GTmax} shown at the instantaneous temperatures of 10°C and 30°C (Table 7). Trends in the percentage of P_{GTmax} at 10°C and 30°C among species ranged from that of the temperate species *E. lucida*, which showed its highest percentages when grown at the day temperatures of 14°C and 22°C, to the tropical species *A. scholaris*, which showed its highest percentages when grown at the day growth temperatures of 22°C and 30°C. Both the temperate and tropical groups showed their highest percentages of P_{GTmax} at 10°C and 30°C when grown at 22°C/14°C. However, the temperate group showed no significant change in these percentages with growth temperature whereas the tropical group showed a significantly reduced percentage of P_{GTmax} at 10°C and 30°C when grown at 14°C/6°C (Fig. 3).

Table 3 Maximum rates of P_{max} (P_{GTmax}), optimum growth temperatures for P_{max} (GT_{opt}) and the span of temperatures over which at least 80% of P_{GTmax} was shown (GT_{span}) for individual species. Parameters are means of two runs with standard errors in brackets. Shared superscripts represent non-significant groupings (P>0.05) of species. *Castanospermum australe* does not have standard errors as it was only measured during the second run of the experiment

Species	P_{GTmax} (μmol m^{-2} s^{-1})	GT_{opt} (°C)	GT_{span} (°C)
E. lucida	5.40 (0.09)^{b}	18.7 (0.1)^{a}	11.8 (0.3)^{ab}
N. cunninghamii	6.87 (0.17)^{a}	21.5 (0.1)	15.7 (1.2)^{a}
T. laurina	10.78 (0.14)	25.4 (0.1)^{cd}	15.2 (0.9)^{ab}
A. smithii	6.07 (0.13)^{ab}	19.5 (0.1)^{a}	13.6 (1.6)^{ab}
S. woollsii	6.76 (0.32)^{a}	24.2 (0.2)^{b}	10.5 (1.1)^{ab}
H. trifoliolata	6.24 (0.04)^{ab}	24.5 (0.2)^{bc}	9.7 (0.3)^{ab}
C. australe	3.26	26.3 ^{de}	9.4^{ab}
A. scholaris	9.39 (0.19)	27.3 (0.2)^{e}	8.6 (0.4)^{b}
Species F	143	579	8.25
Species P	<0.01	<0.01	0.01
Run F	1.02	2.04	1.55
Run P	0.35	0.20	0.26

Table 4 The increase in T_{opt} with increasing day growth temperature (α) for individual species. The statistics for the linear regressions from which these values were obtained are also given

Species	α (°C/°C)	F	P
E. lucida	–	1.00	0.35
N. cunninghamii	0.17	22.0	<0.01
T. laurina	0.10	24.0	<0.01
A. smithii	0.35	35.5	<0.01
S. woollsii	0.25	37.9	<0.01
H. trifoliolata	0.16	16.4	<0.01
C. australe	0.40	14.0	0.01
A. scholaris	0.48	36.1	0.01

Table 6 The span of instantaneous temperatures over which at least 80% of P_{max} was shown by the species. Values are means of the two runs with standard errors in brackets

Species	Growth temperature regime (day /night)		
	14°C/6°C	22°C/14°C	30°C/22°C
E. lucida	20.0 (0.7)	19.4 (0.9)	18.6 (0.7)
N. cunninghamii	19.9 (0.7)	19.1 (0.6)	18.8 (0.8)
T. laurina	15.6 (0.8)	15.9 (1.0)	16.0 (1.0)
A. smithii	17.1 (1.0)	18.5 (0.7)	19.1 (0.7)
S. woollsii	17.6 (0.4)	19.7 (0.6)	17.8 (1.3)
H. trifoliolata	18.2 (1.0)	17.0 (0.8)	16.9 (1.0)
C. australe	16.1	16.0	13.9
A. scholaris	15.9 (1.1)	17.4 (1.2)	16.6 (1.2)
Species F	5.73	1.41	3.08
Species P	0.02	0.34	0.10
Run F	7.77	0.19	0.77
Run P	0.03	0.67	0.41

Table 5 The optimum temperatures of net photosynthesis (T_{opt}) for the climate groups grown under different temperature regimes. Values of T_{opt} are means of four species with standard errors in brackets

Climate group	Growth temperature regime (day /night)				
	14°C/6°C	19°C/11°C	22°C/14°C	25°C/17°C	30°C/22°C
Temperate	20.4 (1.2)	20.5 (1.2)	21.2 (1.2)	21.7 (1.2)	23.0 (1.5)
Tropical	21.0 (1.2)	22.6 (0.6)	24.9 (0.7)	24.9 (0.4)	25.9 (0.1)
F	0.09	2.38	7.37	6.79	3.85
P	0.77	0.17	0.03	0.04	0.10

Table 7 The percentage of P_{GTmax} shown at the instantaneous temperatures (*IT*) of 10°C and 30°C by leaves of the species grown under different temperature regimes. Values are means of two runs with standard errors in brackets except for *C. australe*, which was only measured, in the second run. Shared superscripts represent no significant difference ($P<0.05$) between those growth temperatures

Species	IT	Growth temperature regime			F	P
		14°C/6°C	22°C/14°C	30°C/22°C		
E. lucida	10	68.9 (1.5)[a]	72.6 (0.7)[a]	47.0 (1.3)	120	<0.01
	30	60.2 (3.0)[a]	69.6 (1.1)[a]	44.8 (1.7)	36.0	0.01
N. cunninghamii	10	56.0 (5.5)	77.3 (2.0)	56.4 (4.4)	9.71	0.05
	30	54.6 (0.4)[b]	72.6 (3.7)[a]	68.0 (1.7)[ab]	12.9	0.03
T. laurina	10	30.0 (2.0)	58.2 (1.7)	45.2 (0.2)	84.6	<0.01
	30	46.5 (3.4)	88.5 (0.4)[a]	87.3 (1.4)[a]	140	<0.01
A. smithii	10	51.3 (0.7)	59.3 (1.1)	35.4 (3.6)	2.90	0.20
	30	58.2 (1.7)[b]	71.7 (0.8)[a]	64.5 (0.2)[ab]	39.2	0.01
S. woollsii	10	17.0 (2.4)[b]	60.1 (6.2)[a]	39.7 (0.2)[ab]	25.5	0.01
	30	22.6 (0.5)[b]	93.5 (6.5)[a]	69.5 (1.3)[ab]	13.2	0.03
H. trifoliolata	10	21.4 (4.7)	45.4 (3.8)	36.7 (5.9)	6.13	0.09
	30	28.0 (6.3)[b]	89.3 (5.7)[a]	66.6 (7.6)[ab]	16.4	0.02
C. australe	10	20.0	42.1	23.4		
	30	17.5	63.8	63.7		
A. scholaris	10	24.5 (1.7)	37.5 (2.1)[a]	37.9 (1.5)[a]	78.3	0.02
	30	30.4 (0.1)	82.7 (2.1)[a]	78.9 (0.8)[a]	251	<0.01

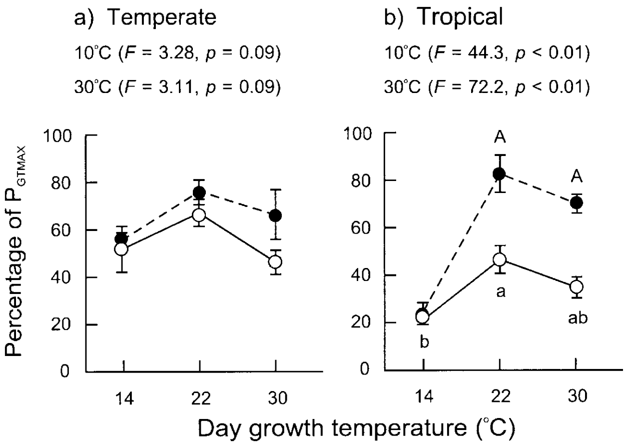

Fig. 3 Percentage of P_{GTmax} shown at the instantaneous temperatures of 10°C (open circle) and 30°C (filled circle) by leaves of the climate groups grown under the 14°C/6°C, 22°C/14°C and 30°C/22°C regimes. Values are means of four species with *bars* representing one standard error. Letters denote non-significant groupings of means. The data were arcsine transformed for analysis

Discussion

The tropical species showed maximum net photosynthesis at a higher growth temperature than the temperate species. This suggests an adaptation of photosynthetic rates in tropical species to the higher maximum and mean temperatures of their climate (Table 2). The majority of the species showed maximum net photosynthesis at growth temperatures lower than those of the warmest quarter of their climates and therefore consistent with temperatures experienced by leaves developed early in the growing season. Previous comparisons of photosynthetic plasticity among tropical and temperate species have been restricted to herbaceous species and differences in the growth temperature for maximum net photosynthesis among species were not always consistent with their climatic origins (Paul et al. 1990; Scott 1970). The difference between the temperate and tropical rainforest species follows the trend for species from cool climates to show maximum net photosynthesis at lower growth temperatures than species from hot climates (Berry and Björkman 1980). However, previous comparisons of species have tended to use only two extreme growth temperatures, which show the differing tolerances of species but does not allow accurate estimates of the growth temperature for maximum net photosynthesis (e.g. Björkman et al. 1975; Monson et al. 1983; Paul et al. 1990). By comparison, this study clearly shows a difference in the growth temperature for maximum net photosynthesis among species from contrasting climates.

The temperate species maintained closed to maximum net photosynthesis over a larger span of growth temperatures than the tropical species. That is, the tropical species showed greater reductions in maximum net photosynthesis at suboptimal growth temperatures. Similarly, several desert evergreen species, which are exposed to a highly seasonal climate, show close to maximum net photosynthesis over a broader range of growth temperatures than desert annuals or coastal species (Björkman et al. 1975; Mooney et al. 1978; Pearcy 1976). The response of the tropical species is consistent with Janzen's (1967) argument that small seasonal and day-to-day changes in temperature within the tropics have allowed plants to become more narrowly adapted to the conditions. Therefore, the ability of the temperate group to adjust maximum net photosynthesis to a greater range of growth temperatures than the tropical group is likely to be an adaptation to the greater seasonal variation in their climate. This ability is consistent with the greater cold tolerance of temperate species than tropical species (Sakai and Larcher 1987) and the observation that many cool climate species show maximum net photosynthesis at temperatures higher than prevailing leaf temperatures (Berry and Björkman 1980).

Previous studies have found that species exposed to greater seasonal variation in temperature show greater shifts in temperature optima (Björkman et al. 1978; Monson et al. 1983; Strain et al. 1976). In contrast, the tropical species in this study, from the less seasonal climate, showed greater shifts in the optimum temperature for net photosynthesis than the temperate species. However, the ability of a species to maintain close to maximum net photosynthesis over a wide range of instantaneous temperatures reduces the need for adjustments in temperature optima (e.g. Hallgren et al. 1982; Williams and Black 1993). Therefore, species that show no adjustment in their optimum temperature for net photosynthesis with growth temperature are not necessarily from climates that have low seasonal variation in temperature. The larger shifts in temperature optima shown by the tropical species compared with the temperate species were associated with greater reductions in maximum net photosynthesis. This type of response cannot be taken as a greater photosynthetic plasticity, instead it indicates an inability to maintain normal photosynthetic function at low temperatures.

Larcher (1980) records that optimum temperatures for net photosynthesis of tropical trees are 25–30°C, whereas optimum temperatures for temperate evergreen trees are 10–25°C. However, in many species the optimum temperature for net photosynthesis has been shown to change with growth temperature (e.g. Slatyer 1977; Strain et al. 1976). In this study, the tropical species showed maximum net photosynthesis at higher instantaneous temperatures than the temperate species only under moderate growth temperatures. Therefore, the often-cited differences in temperature optima for net photosynthesis between tropical and temperate species may only be true when measured under conditions representative of their native environments.

The temperate and tropical species showed maximum net photosynthesis over a similar range of instantaneous temperatures. The span of the photosynthetic response to instantaneous temperature has been related to the seasonal and diurnal changes of a species' climate (Battaglia et al. 1996; Read 1990). Some of the broadest photosynthetic responses to temperature are shown by shrubs from Mediterranean-type ecosystems, which are characterized by large seasonal changes in temperature (Mooney et al. 1983; Oechel et al. 1981). The small differences in temperature span among the study species seem to reflect the similar diurnal temperature ranges of the species and not the differences in seasonal variation in temperature.

Growing plants at hot or cold temperatures often improves their photosynthetic performance at that temperature (e.g. Forseth and Ehleringer 1982; Vallejos and Pearcy 1987). In the rainforest species of this study, the highest rates of net photosynthesis at extreme temperatures were shown in leaves grown under moderate temperatures. The moderate temperature regime (22°C/14°C) was the closest to the optimum growth temperature for maximum net photosynthesis (20–27°C) and the optimum instantaneous temperature for maximum net photosynthesis (19–26°C) for the majority of species. Therefore, photosynthetic responses at extreme temperatures appear to simply follow the response of maximum net photosynthesis to growth temperature. Temperate species were able to maintain similar photosynthetic rates at extreme temperatures under the three growth temperatures, whereas the tropical species showed significant reductions in photosynthetic rates in leaves developed under 14°C/6°C. This is consistent with the limited exposure of tropical species to low temperatures in their native climates.

The important differences found between the temperate and tropical species were the lower growth temperature for maximum net photosynthesis and the greater span of growth temperatures over which this rate was maintained in temperate species. These differences in photosynthetic plasticity are consistent with differences in acclimation potential found between other temperate and tropical tree species (Hill et al. 1988; Read 1990). Furthermore, they are consistent with differences in photosynthetic plasticity among species from climates differing in the magnitude and seasonality of temperature (Björkman et al. 1975; Mooney et al. 1978; Pearcy 1976). The present findings suggest that temperate tree species maintain high rates of photosynthesis over a wide range of temperatures whereas tropical tree species maintain maximum net photosynthesis over a narrow range of high temperatures. The narrower temperature tolerance of tropical tree species may make them more susceptible than temperate tree species to the predicted increases in global temperatures. Whether these differences in net photosynthesis translate into the overall growth response to temperature will be discussed in a future paper.

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