

# Photosynthetic capacity and temperature responses of photosynthesis of rubber trees (*Hevea brasiliensis* Müll. Arg.) acclimate to changes in ambient temperatures

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**Abstract** The aim of this study was to assess the temperature response of photosynthesis in rubber trees (*Hevea brasiliensis* Müll. Arg.) to provide data for process-based growth modeling, and to test whether photosynthetic capacity and temperature response of photosynthesis acclimates to changes in ambient temperature. Net CO<sub>2</sub> assimilation rate (*A*) was measured in rubber saplings grown in a nursery or in growth chambers at 18 and 28°C. The temperature response of *A* was measured from 9 to

45°C and the data were fitted to an empirical model. Photosynthetic capacity (maximal carboxylation rate, *V*<sub>cmax</sub>, and maximal light driven electron flux, *J*<sub>max</sub>) of plants acclimated to 18 and 28°C were estimated by fitting a biochemical photosynthesis model to the CO<sub>2</sub> response curves (*A*–*C*<sub>i</sub> curves) at six temperatures: 15, 22, 28, 32, 36 and 40°C. The optimal temperature for *A* (*T*<sub>opt</sub>) was much lower in plants grown at 18°C compared to 28°C and nursery. Net CO<sub>2</sub> assimilation rate at optimal temperature (*A*<sub>opt</sub>), *V*<sub>cmax</sub> and *J*<sub>max</sub> at a reference temperature of 25°C (*V*<sub>cmax25</sub> and *J*<sub>max25</sub>) as well as activation energy of *V*<sub>cmax</sub> and *J*<sub>max</sub> (*E*<sub>aV</sub> and *E*<sub>aJ</sub>) decreased in individuals acclimated to 18°C. The optimal temperature for *V*<sub>cmax</sub> and *J*<sub>max</sub> could not be clearly defined from our response curves, as they always were above 36°C and not far from 40°C. The ratio *J*<sub>max25</sub>/*V*<sub>cmax25</sub> was larger in plants acclimated to 18°C. Less nitrogen was present and photosynthetic nitrogen use efficiency (*V*<sub>cmax25</sub>/*N*<sub>a</sub>) was smaller in leaves acclimated to 18°C. These results indicate that rubber saplings acclimated their photosynthetic characteristics in response to growth temperature, and that higher temperatures resulted in an enhanced photosynthetic capacity in the leaves, as well as larger activation energy for photosynthesis.

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rate · Optimal temperature · Temperature acclimation

## Introduction

Temperature is an important factor affecting photosynthesis, and understanding the temperature response of photosynthesis is a prerequisite for modelers to predict the responses of canopies to global climate change. The

biochemical photosynthesis model of Farquhar et al. (1980) is widely used to describe responses of photosynthesis to environment. This model captures photosynthesis with two major parameters: the maximal carboxylation rate ( $V_{\text{cmax}}$ ) and the maximal light-driven electron flux ( $J_{\text{max}}$ ). These two parameters are influenced: (1) by leaf structure and chemistry, particularly by leaf nitrogen content (Harley et al. 1992; Niinemets and Tenhunen 1997; Le Roux et al. 1999; Niinemets et al. 1999b) and (2) by leaf temperature (Leuning 1997; Walcroft and Kelliher 1997; Niinemets et al. 1999a; Dreyer et al. 2001; Medlyn et al. 2002a, b).  $V_{\text{cmax}}$  and  $J_{\text{max}}$  vary widely among species (Wullschlegel 1993; Dreyer et al. 2001; Medlyn et al. 2002a) and within species according to growth conditions (Berry and Björkman 1980; Ferrar et al. 1989; Bunce 2000).

Growth temperature can induce acclimation of photosynthesis, e.g., change the photosynthetic capacity or the temperature response of photosynthesis, or both (Bunce 2000; Medlyn et al. 2002a; Onoda et al. 2005a, b; Yamori et al. 2005; Atkin et al. 2006b; Kattge and Knorr 2007; Sage and Kubien 2007). Plants are thought to acclimate to the growth temperature to achieve efficient photosynthesis at the new temperature (Berry and Björkman 1980; Sage and Kubien 2007). The potential for acclimation to different growth temperatures probably differs among species (Atkin et al. 2006b), but the amount of data in support of this remains scarce.

This scarcity is more evident for tropical tree species (Kattge and Knorr 2007). In general, photosynthesis in tropical species operates without irreversible damage between 15 and 45°C (Sage and Kubien 2007, and references therein). Rubber (*Hevea brasiliensis* Müll. Arg.) is a tropical economic tree crop, planted mainly in south-east Asia. Rubber tree plantations are currently expanding to non-traditional areas such as Northern and Northeastern Thailand, Yunnan in China or Mato Grosso in Brazil, where trees encounter more extreme (cold and hot) temperatures. Environmental conditions such as temperature influence the growth of rubber and latex yield (Raj et al. 2005, and references therein). Alam et al. (2005) showed that rubber trees can acclimate to different agro-climatic conditions, under colder and warmer climates. However, little is known about net CO<sub>2</sub> assimilation rate of rubber leaves in a wide range of temperatures, covering both hot and potentially cold temperature in new plantation areas. Moreover, data necessary to assess temperature acclimation of photosynthesis using Farquhar's model in rubber trees are lacking.

To understand how photosynthesis responds and acclimates to growth temperature in rubber tree, following questions were addressed:

1. What is the temperature response of net CO<sub>2</sub> assimilation rate ( $A$ ) of rubber grown in a nursery in Thailand and in a growth chamber at 28°C?
2. Does photosynthetic capacity as described by the model parameters  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  at a reference temperature of 25°C change after an acclimation to different growth temperatures?
3. Does the temperature response of  $A$  and of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  as described by optimal temperature and activation energy change with growth temperatures?

These questions were answered with: (1) data from an experiment with saplings of rubber trees grown in a nursery at ambient temperature in Thailand for which  $A$  was measured over the range 23–45°C; (2) data from an experiment with saplings of rubber trees grown in a growth chamber at 28°C in France for which  $A$  was recorded over a temperature range 9–38°C; and (3) data from an experiment with saplings of rubber tree acclimated to 18 or to 28°C in a growth chamber in France for which  $A$ – $C_i$  curves were measured at six different leaf temperatures from 15 to 40°C, to assess changes in photosynthetic capacity with growth temperature.

## Materials and methods

Experiments were conducted on rubber (*Hevea brasiliensis* Müll. Arg.) with intact, fully expanded, 1–2 months old leaves. Gas exchange was measured with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, Nebraska, USA) equipped with a blue–red LED light source (LI-6400-02B) and CO<sub>2</sub> injection system (LI-6400-01).

Experiment 1: temperature response of net CO<sub>2</sub> assimilation rate of rubber saplings grown in a nursery in Thailand

Budded scions of rubber were planted in 50 l pots filled with Pakchong soil series composed of sand (24.5%), silt (6.3%), clay (69.2%) and organic matter (2.7%). All plants were grown in a nursery under natural conditions at the Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok, Thailand (latitude: 13.85°N, longitude: 100.75°E). Ambient temperature, relative air humidity and PPFD were recorded with a WatchDog model 900ET Weather Station (Spectrum technologies, Inc). Mean ambient temperature, relative humidity and daily photosynthetic photon flux density varied between 27 and 38°C, 20–90%, 10–1,600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, during the study period.

All plants were irrigated daily. Temperature response of net CO<sub>2</sub> assimilation rate ( $A$ ) was measured during 2006, between 23 and 45°C, on one leaf of four 3-month-old saplings. To reach the lowest temperatures, ambient air was cooled down with a custom air-temperature control system

constructed at Kasetsart University during 2005. The cooling system consisted of an air conditioner and an air blower installed inside a closed container. Temperature of the control system was set between 17 and 30°C. Leaf temperature was increased gradually with 1–2°C steps between 23 and 45°C. Photosynthesis measurements were logged after 15–20 min stabilization at each temperature step. Measurements were made under saturating photosynthetic photon flux density (PPFD, 1,200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and ambient  $\text{CO}_2$  mole fraction of 380  $\mu\text{mol mol}^{-1}$ .

#### Experiment 2: temperature response of *A* of a rubber sapling grown in a growth chamber

One 3-month-old rubber sapling was obtained from the Michelin Company at Clermont-Ferrand, France. It was grown in a 33 l pot filled with a 1/2 (v/v) mixture of peat and clay soil, and acclimated during 2 months (2006) in a growth chamber at PIAF, INRA, Clermont-Ferrand, France. The growth chamber was set at 28°C, 12 h photoperiod, 250  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD at leaf level and 80% relative humidity. The sapling was watered and fertilized two–three times a week with 1.5 l, 20/20/20 N/P/K Plant-Prod (Plant Products Co. Ltd., Ontario, Canada) at 0.5  $\text{g l}^{-1}$ .

Temperature response of photosynthesis was recorded on six leaves at 1–2°C intervals between 9 and 38°C. The growth chamber was set at  $10 \pm 1$ ,  $20 \pm 1$  and  $32 \pm 1^\circ\text{C}$  for leaf temperature ranges 9–16, 17–25 and 26–38°C, respectively. At each temperature step, photosynthesis measurements were logged after 5–10 min stabilization under a saturating PPFD of 1,200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and an ambient  $\text{CO}_2$  mole fraction of 350  $\mu\text{mol mol}^{-1}$ .

#### Experiment 3: temperature response of *A*, $V_{\text{cmax}}$ and $J_{\text{max}}$ of rubber saplings acclimated to different temperatures

The experiment was performed during 2007 at PIAF, INRA, Clermont-Ferrand, France. Four potted 3-month-old rubber saplings obtained from Michelin Company were grown in 33 l pots filled with a 1/2 (v/v) mixture of peat and clay soil and continuously drip-irrigated in a greenhouse, under 28/20°C (day/night), relative humidity of 80% (day/night) and natural PPFD in the greenhouse at Blaise Pascal University, Clermont-Ferrand, France during 2 months before the experiment.

#### Temperature acclimation treatment

The saplings were transferred from the greenhouse to two growth chambers at 18 and 28°C, respectively, for at least 3 weeks acclimation before measurements. Conditions

were: 12 h photoperiod at constant temperature during day and night, PPFD at leaf level ca. 250  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and 80% relative humidity. Saplings were watered every day and fertilized two–three times a week as in experiment 2.

#### $\text{CO}_2$ response curves

$\text{CO}_2$  response ( $A-C_i$ ) curves were measured at leaf temperatures ( $\pm 0.5^\circ\text{C}$ ) of 15, 22, 28, 32, 36 and 40°C, except in one case where the two highest temperatures resulted in complete stomatal closure. PPFD was set at 1,200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  except at 22, 28 and 32°C for the saplings acclimated to 18°C where PPFD was set at 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  as light saturation level declined.

$A-C_i$  curves were recorded at each temperature by transferring the saplings from the acclimation growth chamber to a third growth chamber used only for measurements, under similar micro-environments except for temperature. The saplings and LI-6400 system were kept for at least 1 h for equilibration at the new temperature before performing gas exchange measurements. The plant was moved back to the acclimation chamber after the end of measurement sequence each day.

$A-C_i$  curves started from an ambient  $\text{CO}_2$  concentration of 360  $\mu\text{mol mol}^{-1}$ . The measurement was recorded when net  $\text{CO}_2$  assimilation rate (*A*) and stomatal conductance ( $g_s$ ) stabilized, after about 20–30 min. External  $\text{CO}_2$  was set in 10–14 steps from 360 to 50  $\mu\text{mol mol}^{-1}$  and from 360 to 1,400–1,800  $\mu\text{mol mol}^{-1}$  to obtain  $A_c$  (*A* limited by RuBP carboxylation) and  $A_j$  (*A* limited by RuBP regeneration). Stomatal conductance decreased quickly at high  $\text{CO}_2$  and values of *A* were discarded whenever  $g_s$  was less than 0.040  $\text{mol m}^{-2} \text{s}^{-1}$ . The same leaf was measured at all temperatures and four to five leaves were used per tree.

At the end of the experiment, leaves were harvested. Chlorophyll content was assessed with a portable chlorophyll meter (SPAD-502; Konica Minolta Sensing, Inc., Osaka, Japan). Leaf area was measured with a leaf area meter, LI-3100A (LI-COR Inc., Lincoln, NE, USA). Leaves were dried at 70°C for 48 h. Leaf mass per area (LMA) was calculated from measurements of leaf area and dry weight. Leaf carbon and nitrogen were analyzed with an elemental microanalyser (Carlo Erba, model EA 1108, Milano, Italy).

#### Data analysis

##### *Temperature response of net $\text{CO}_2$ assimilation rate*

The response curves to temperature of net  $\text{CO}_2$  assimilation rate at ambient  $\text{CO}_2$  concentration were fitted by non linear least squares regression with an empirical model (June et al. 2004), Eq. 1:

$$P(T) = P(T_{\text{opt}})e^{-\left(\frac{T_{\text{opt}}-T}{\Omega}\right)^2} \quad (1)$$

where  $T_{\text{opt}}$  is the optimal temperature ( $^{\circ}\text{C}$ ),  $T$  is the leaf temperature ( $^{\circ}\text{C}$ ),  $\Omega$  is the shape parameter,  $P(T)$  and  $P(T_{\text{opt}})$  are the values of the parameter of interest (net  $\text{CO}_2$  assimilation rate) at ambient and optimal temperature, respectively.

*CO<sub>2</sub> response curves fit and estimation of apparent  $V_{\text{cmax}}$  and  $J_{\text{max}}$*

$A-C_i$  curves were fitted according to the Farquhar's model (Farquhar et al. 1980; Farquhar and von Caemmerer 1982; Harley and Tenhunen 1991), by non-linear least squares regression (Dreyer et al. 2001), assuming infinite internal conductance ( $g_i$ ), i.e., the partial pressure at carboxylation sites equals that in substomatal cavities. The parameter set from Bernacchi et al. (2001), suitable for  $A-C_i$  curve fitting with infinite  $g_i$ , was used. The fitting procedure yielded therefore estimates of apparent  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (Ethier and Livingston 2004). An attempt to fit  $A-C_i$  curve to a model with a finite  $g_i$  allowing to simultaneously fit  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  and  $g_i$  as described in Ethier and Livingston (2004) induced large uncertainties in the parameters; the resulting estimates were therefore discarded.

*Temperature response of photosynthetic model parameters ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ )*

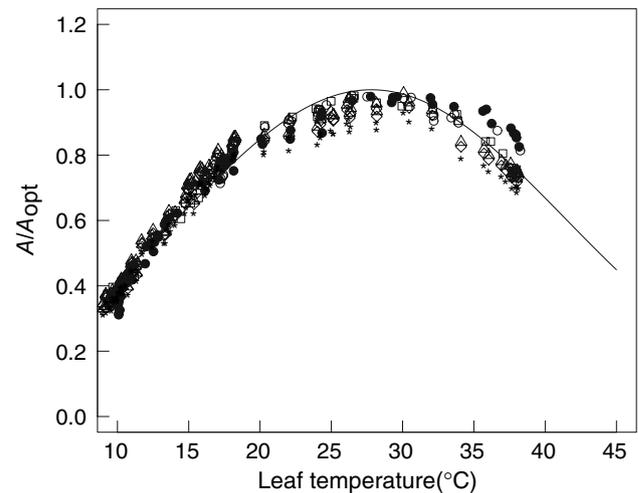
Temperature responses of the parameters were modeled according to the Arrhenius equation:

$$P(T) = P(T_{\text{ref}})e^{\frac{E_a}{R}\left(\frac{1}{T_{\text{ref}}} - \frac{1}{T}\right)} \quad (2)$$

where  $P(T)$  is the parameter of interest,  $T_{\text{ref}}$  is the reference temperature of  $25^{\circ}\text{C}$  (298.15 K),  $P(T_{\text{ref}})$  is the parameter of interest at reference temperature,  $E_a$  is the activation energy ( $\text{J mol}^{-1}$ ),  $R$  is the gas constant ( $8.314 \text{ J K}^{-1} \text{ mol}^{-1}$ ) and  $T$  is the leaf temperature (K).

The response curves of photosynthetic parameters ( $V_{\text{cmax}}$ ,  $J_{\text{max}}$ ) were fitted with the Arrhenius function (Eq. 2) by weighted non linear least squares fit. Data points, i.e., estimates of apparent  $V_{\text{cmax}}$  or  $J_{\text{max}}$  at each measurement temperature were weighted by the reciprocal of their estimation variance obtained from the fit of  $A-C_i$  curves.

Leaves on a single sapling were regarded as pseudo-replicates, and there were two saplings per treatment, i.e., two real replicates. In order to test acclimation effects, the estimates from all saplings and leaves were pooled into one single fit, using dummy variables for each sapling and leaf, following the procedure described in Dreyer et al. (2001),



**Fig. 1** Example of temperature response of net  $\text{CO}_2$  assimilation rate ( $A$ ) relative to values at optimal temperature ( $A_{\text{opt}}$ ) of six leaves grown in a growth chamber at  $28^{\circ}\text{C}$ . Leaf temperature ranged from 9 to  $38^{\circ}\text{C}$ .  $A$  was measured at an ambient  $\text{CO}_2$  mole fraction of  $350 \mu\text{mol mol}^{-1}$ . Different symbols represent different leaves

as to obtain an estimate of the parameter ( $V_{\text{cmax}}$  or  $J_{\text{max}}$ ) at  $25^{\circ}\text{C}$  for each leaf and an estimate of activation energy for each sapling  $\times$  acclimation temperature combination. It is therefore assumed that leaves from the same individual under the same acclimation temperature share identical activation energies. Then an analysis of contrasts was performed for testing specific hypotheses.

A similar procedure using dummy variables and pooled data was used in experiment 2 for fitting the empirical temperature model and deriving optimal temperature ( $T_{\text{opt}}$ ) and net assimilation rate at optimal temperature ( $A_{\text{opt}}$ ), here assuming the same optimal temperature and shape parameter for all leaves of an individual.

## Results

Temperature response and acclimation of net  $\text{CO}_2$  assimilation rate ( $A$ )

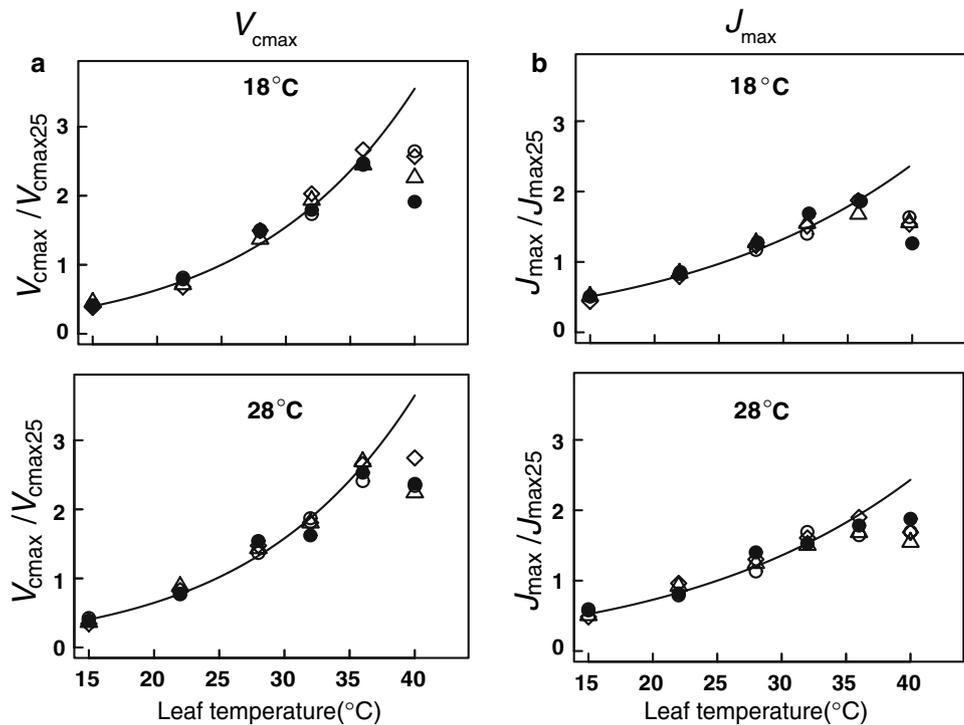
The standardized values  $A/A_{\text{opt}}$  displayed the temperature response presented in Fig. 1. Optimal temperature ( $T_{\text{opt}}$ ) was similar in plants grown at  $28^{\circ}\text{C}$  in a growth chamber (experiments 2 and 3) or at higher but variable temperature ( $>27^{\circ}\text{C}$ ) in Thailand (Table 1).  $T_{\text{opt}}$  and  $A_{\text{opt}}$  were lower in saplings acclimated to 18 than to  $28^{\circ}\text{C}$ .  $\Omega$  was also lower in plants grown at  $18^{\circ}\text{C}$ , indicating a narrower peak in the temperature response, i.e.,  $A$  decreased steeper around the optimal temperature. There was no difference between the two trees within each treatment.

**Table 1** Mean  $\pm$  SE (nursery,  $n = 4$  saplings; exp (experiment) 2,  $n = 6$  leaves; exp 3,  $n = 2$  saplings  $\times$  4–5 leaves) of optimal temperature for net CO<sub>2</sub> assimilation rate ( $T_{opt}$ ) of rubber saplings acclimated to different temperatures ( $T_{growth}$ ), of the shape-coefficient of the temperature response ( $\Omega$ ) and of net CO<sub>2</sub> assimilation rate ( $A$ ) at  $T_{opt}$  ( $A_{opt}$ )

	Exp 1 Nursery	Exp 2 Growth chamber	Exp 3 Growth chamber	
$T_{growth}$ (°C)	27–38	28	18	28
$T_{opt}$ (°C)	29.4 $\pm$ 0.1	27.8 $\pm$ 0.1	25.0 $\pm$ 0.4 <sup>a</sup>	30.3 $\pm$ 0.3 <sup>b</sup>
$\Omega$	18.1 $\pm$ 0.3	19.2 $\pm$ 0.2	17.1 $\pm$ 1.0 <sup>a</sup>	21.5 $\pm$ 0.7 <sup>b</sup>
$A_{opt}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	10.1 $\pm$ 0.02	9.0 $\pm$ 0.2	5.3 $\pm$ 0.1 <sup>a</sup>	9.2 $\pm$ 0.1 <sup>b</sup>

Different superscript letters within indicate statistically different values at  $P < 0.001$  using contrast analysis. The three experiments are described in the text

**Fig. 2** Examples of temperature response of (a)  $V_{cmax}$  (expressed as  $V_{cmax}$  relative to  $V_{cmax25}$ ) and (b) of  $J_{max}$  (expressed as  $J_{max}$  relative to  $J_{max25}$ ) in rubber acclimated to 18 or to 28°C. The values of  $V_{cmax}$  and  $J_{max}$  were estimated by fitting the temperature response functions to  $A-C_i$  curves obtained at six different temperatures.  $V_{cmax}$  and  $J_{max}$  were estimated at six different temperatures ranged from 15 to 40°C and normalized to the mean value at 25°C ( $V_{cmax25}$  and  $J_{max25}$ ;  $n = 4-5$  leaves). Different symbols represent different leaves



Temperature response and acclimation of photosynthetic capacity

Examples of temperature responses of apparent  $V_{cmax}$  and  $J_{max}$  are displayed in Fig. 2. The estimates at 40°C were discarded from the temperature adjustment as they already deviated from the increasing trend, demonstrating that the temperature optimum was probably below but close to 40°C. The number of points describing the decline was too small for an accurate estimate of the deactivation energy or the entropy terms needed to account for deactivation at high temperature (Niinemets and Tenhunen 1997; Dreyer et al. 2001; Medlyn et al. 2002a). It was therefore assumed that only negligible deactivation occurred at temperatures below 36°C. The optimal temperature of  $V_{cmax}$  and  $J_{max}$  for

saplings grown at both temperatures was therefore not estimated but it may be safely assumed it was notably above 36°C.

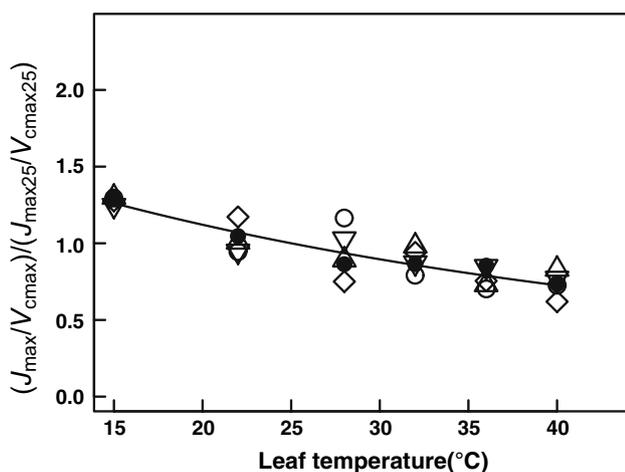
Values of photosynthetic capacity at a reference temperature (25°C,  $V_{cmax25}$  and  $J_{max25}$ ) were significantly lower under the lower growth temperature (Table 2) and the difference was approximately 50%. The activation energy of  $V_{cmax}$  and  $J_{max}$  was larger in the individuals acclimated to 28 than to 18°C (Table 2). An example of the temperature response of the ratio of  $J_{max}$  to  $V_{cmax}$  in saplings is shown in Fig. 3. The ratio decreased as expected with increasing temperature. The ratio of  $J_{max25}$  to  $V_{cmax25}$  was higher in the individuals acclimated to 18 than to 28°C (Table 2).

Leaves of individuals acclimated to 18°C turned out to be less green and displayed smaller chlorophyll content per

**Table 2** Photosynthetic capacity at a reference temperature of 25°C (maximal carboxylation rate,  $V_{\text{cmax}25}$  and maximal light-driven electron flux,  $J_{\text{max}25}$ ); temperature response (activation energy,  $E_{\text{aV}}$  and  $E_{\text{aJ}}$  of the two parameters); leaf mass per area ratio (LMA), chlorophyll content measured with a chlorophyll meter (SPAD), leaf nitrogen ( $N_m$ ) and leaf carbon content (C) and photosynthetic nitrogen use efficiency (PNUE) ( $=V_{\text{cmax}25}/N_a$  and  $J_{\text{max}25}/N_a$ ) recorded in saplings acclimated to 18 and 28°C

Parameter	Growth temperature (°C)	
	18	28
$V_{\text{cmax}25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	26.1 $\pm$ 1.8 <sup>a</sup>	43.9 $\pm$ 2.9 <sup>b</sup>
$E_{\text{aV}}$ (kJ mol <sup>-1</sup> )	60.8 $\pm$ 7.2 <sup>a</sup>	68.5 $\pm$ 6.2 <sup>b</sup>
$J_{\text{max}25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	50.8 $\pm$ 9.9 <sup>a</sup>	77.4 $\pm$ 11.2 <sup>b</sup>
$E_{\text{aJ}}$ (kJ mol <sup>-1</sup> )	39.2 $\pm$ 18.5 <sup>a</sup>	50.6 $\pm$ 13.5 <sup>b</sup>
$J_{\text{max}25}/V_{\text{cmax}25}$	1.93 $\pm$ 0.005 <sup>a</sup>	1.79 $\pm$ 0.004 <sup>b</sup>
LMA (g m <sup>-2</sup> )	64.1 $\pm$ 1.4 <sup>a</sup>	52.1 $\pm$ 1.3 <sup>b</sup>
SPAD	41.6 $\pm$ 0.9 <sup>a</sup>	55.6 $\pm$ 0.9 <sup>b</sup>
$N_m$ (%)	2.72 $\pm$ 0.05 <sup>a</sup>	4.08 $\pm$ 0.05 <sup>b</sup>
C (%)	47.4 $\pm$ 0.2 <sup>a</sup>	48.2 $\pm$ 0.2 <sup>b</sup>
$V_{\text{cmax}25}/N_a$ ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	14.8 $\pm$ 0.3 <sup>a</sup>	21.2 $\pm$ 0.3 <sup>b</sup>
$J_{\text{max}25}/N_a$ ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	28.9 $\pm$ 0.9 <sup>a</sup>	37.0 $\pm$ 0.8 <sup>b</sup>

Mean  $\pm$  SE ( $n = 2$  saplings  $\times$  4–5 leaves). Different superscripts indicate statistically difference values at  $P < 0.001$  (for  $J_{\text{max}25}/V_{\text{cmax}25}$ ,  $P = 0.0024$ ) using contrast analysis



**Fig. 3** Example of temperature response of the ratio  $J_{\text{max}}$  to  $V_{\text{cmax}}$  ( $J_{\text{max}}/V_{\text{cmax}}$ ) (expressed as  $J_{\text{max}}/V_{\text{cmax}}$  to  $J_{\text{max}25}/V_{\text{cmax}25}$ ) in rubber acclimated to 28°C. Different symbols represent different leaves (4–5 leaves)

unit leaf area as indicated by the SPAD values. LMA was higher in plants grown at 18 than at 28°C. Nitrogen content ( $N_m$ ) was significantly smaller in plants grown at 18°C (Table 2). Photosynthetic nitrogen use efficiency (PNUE) expressed as  $V_{\text{cmax}25}/N_a$  and  $J_{\text{max}25}/N_a$ , where  $N_a$  is the leaf nitrogen content per unit leaf area, was significantly smaller in saplings grown at 18°C (Table 2).

## Discussion

### Temperature acclimation

A period of temperature acclimation of at least 3 weeks (to 18 and 28°C) as used in the present study for young and fully expanded leaves was sufficient to induce significant differences in photosynthesis and in its responses to temperature in our rubber saplings. Earlier studies reported that acclimation of the photosynthetic apparatus requires a period of days or weeks (Berry and Björkman 1980, and references therein).

### Temperature response and acclimation of net CO<sub>2</sub> assimilation rate and photosynthetic capacity

In general, optimal temperature for net CO<sub>2</sub> assimilation rate ( $A$ ) is around 30°C for tropical species (Mason et al. 2001). In the present study, optimal temperature ( $T_{\text{opt}}$ ) for  $A$  changed at different growth temperatures.  $T_{\text{opt}}$  for  $A$  of rubber saplings grown in a nursery as well as in a growth chamber at 28°C was in the range 27–33°C as reported in earlier studies (Rao et al. 1998, and references therein). Rubber saplings grown at lower temperature displayed a lower optimal temperature for  $A$ . This result is in agreement with many earlier results (Slatyer, 1977a, b; Slatyer and Morrow 1977; Berry and Björkman 1980; Ferrar et al. 1989; Yamori et al. 2005; Hikosaka et al. 2006) showing that plants do acclimate their physiology so that optimal temperature for  $A$  becomes closer to growth temperature. The potential of photosynthesis acclimation to temperature varies among species. For example, winter wheat (*Triticum aestivum* L. cv Norin No. 61) had an extremely high potential for temperature acclimation of photosynthesis, as the optimal temperature for photosynthesis was 15–20°C, 25–30°C and around 35°C in plants grown at 15, 25 and 35°C, respectively (Yamasaki et al. 2002). In rubber, this potential for acclimation was not as large, as optimal temperature remained about 2–7°C higher than growth temperature in the present study. Not only optimal temperature, but also the shape of the temperature response curve of net CO<sub>2</sub> assimilation rate, similarly to results of June et al. (2004). Therefore, photosynthesis of such plants decreases rapidly whenever temperature differs from the optimum.

In the present study,  $A_{\text{opt}}$ ,  $V_{\text{cmax}25}$  and  $J_{\text{max}25}$  changed with acclimation temperature and were lower after acclimation at 18 than at 28°C. Photosynthetic capacity declines significantly in rubber individuals acclimated to lower temperatures as reported earlier in other species (Makino et al. 1994; Medlyn et al. 2002b; Warren 2008).

Unfortunately, the initial values of photosynthetic capacity had not been assessed before transferring the plants to the temperature treatments, and we are unable to quantify accurately the change induced by 3 weeks acclimation to lower temperatures. Nevertheless, the observed changes in nitrogen content and in LMA could help interpret the lower photosynthetic capacity of individuals acclimated at 18°C. Photosynthetic capacity is related to leaf nitrogen content (Walcroft and Kelliher 1997; Medlyn et al. 2002b) as  $V_{\text{cmax}}$  depends on the amount of Rubisco protein and  $J_{\text{max}}$  depends on the amount of thylakoid components (von Caemmerer 2000). The fact that  $V_{\text{cmax}25}$  decreased in parallel with leaf nitrogen suggests that Rubisco concentration decreased in plants acclimated to 18°C. However, the dependence of photosynthetic capacity on leaf nitrogen varies among species (Hikosaka et al. 1998, and references therein), and Rubisco kinetics as well as Rubisco activation state probably acclimate to the growth temperature (Salvucci and Crafts-Brandner 2004; Yamori et al. 2006). In our case, at 18°C not only did the absolute values of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  decrease, but photosynthetic capacity per unit leaf nitrogen (PNUE,  $V_{\text{cmax}25}/N_{\text{a}}$  and  $J_{\text{max}25}/N_{\text{a}}$ ) also decreased. The difference in PNUE may be attributed to the difference in specific activity of Rubisco and nitrogen allocation to Rubisco (Hikosaka et al. 1998; Warren and Dreyer 2006). The allocation of nitrogen is also correlated with LMA. Warren and Dreyer (2006) reported that the internal conductance to CO<sub>2</sub> transfer ( $g_i$ ) can affect the absolute values of photosynthetic capacity and the temperature response of photosynthesis. Temperature is one factor of the variation in  $g_i$ . Therefore, the difference in PNUE of plants grown at different temperatures can also be attributed to temperature induced differences in  $g_i$ .

In the present study, plants with larger LMA (grown at lower temperature, 18°C) had lower photosynthetic capacity and PNUE, which is consistent with other studies in evergreen *Quercus* species (Mediavilla et al. 2001; Takashima et al. 2004). Atkin et al. (2006a) also found that plants grown at low temperature displayed higher LMA than plants grown at warm temperature. Larger LMA after acclimation to 18°C may be due to several factors: (1) an increased allocation of nitrogen to structural proteins, resulting in decreased photosynthetic capacity and PNUE (Takashima et al. 2004); (2) larger accumulation of non-structural carbohydrates (Bertin et al. 1999), particularly starch (Usami et al. 2001), due to impaired growth and decreased translocation.

The optimal temperature for the two components of photosynthetic capacity ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ) was above 36°C and not far from 40°C; this is in the range of values produced by Dreyer et al. (2001) who showed that the optimal temperature ranged between 35.9 and above 45°C for  $V_{\text{cmax}}$  and between 31.7 and 43.3°C for  $J_{\text{max}}$  in seedlings from

seven temperate tree species. Other studies reported that the optimal temperature for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  was 36.6 and 33.3°C, respectively in silver fir seedlings (Robakowski et al. 2002) and 34 and 33.3°C, respectively in cork oak seedlings (Ghouil et al. 2003). Therefore, although rubber is a tropical species, its optimal temperature for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were not higher than in temperate species.

The temperature response of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were also influenced by acclimation temperature. Although actual optimal temperature for the two components was not estimated from our data due to the small number of points above optimum, activation energy of  $V_{\text{cmax}}$  ( $E_{\text{aV}}$ ) and of  $J_{\text{max}}$  ( $E_{\text{aJ}}$ ) was larger in plants acclimated to higher temperature. This result is consistent with several studies (Hikosaka et al. 1999; Onoda et al. 2005b), whereas others found no correlation of  $E_{\text{aV}}$  and  $E_{\text{aJ}}$  with growth temperature (Medlyn et al. 2002b). In the present study, the activation energy was as expected higher for  $V_{\text{cmax}}$  than for  $J_{\text{max}}$  resulting in a decrease in the ratio of  $J_{\text{max}}$  to  $V_{\text{cmax}}$  with increasing temperature.

In general,  $V_{\text{cmax}}$  and  $J_{\text{max}}$  are strongly correlated (Wullschlegel 1993). The change in the balance between RuBP carboxylation and regeneration with growth temperature confirms earlier observations (Hikosaka et al. 1999; Onoda et al. 2005a, b; Yamori et al. 2005). In contrast, Medlyn et al. (2002b) found no change in the ratio of  $J_{\text{max}}$  to  $V_{\text{cmax}}$  with growth temperature. Moreover, the ratio of  $J_{\text{max}}$  to  $V_{\text{cmax}}$  of around 1.7–2.0 in the present study was within a range of 1–3 of many studies that reviewed by Kattge and Knorr (2007).

Our results showing that photosynthesis in rubber can acclimate to growth temperature are consistent with Alam and Jacob (2002) who showed that low temperature stress (around 9.5–19.3°C) inhibits net CO<sub>2</sub> assimilation rate to a larger extent in rubber than in other species acclimated to cool conditions of the mountain in India and with Alam et al. (2005) who indicated that different growth environments affected not only net photosynthetic rate, but also carboxylation efficiency in rubber. Photosynthetic potential was lower in individuals grown in colder environments.

## Conclusion

The present study suggests that rubber has a potential for acclimation of photosynthesis to growth temperature. This involves changes in photosynthetic capacity at a reference temperature ( $V_{\text{cmax}25}$  and  $J_{\text{max}25}$ ) and to a lesser extent (and with less confidence) the temperature response of photosynthetic capacity, thus changing the temperature response of net CO<sub>2</sub> assimilation rate. Although rubber trees grown at 18°C cannot maintain rates of net CO<sub>2</sub> assimilation rate, photosynthetic capacity and leaf nitrogen status close to

those of rubber grown at 28°C, they have the potential to succeed low temperature stress.

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## References

- Alam B, Jacob J (2002) Overproduction of photosynthetic electrons is associated with chilling injury in green leaves. *Photosynthetica* 40:91–95. doi:10.1023/A:1020110710726
- Alam B, Nair DB, Jacob J (2005) Low temperature stress modifies the photochemical efficiency of a tropical tree species *Hevea brasiliensis*: effects of varying concentration of CO<sub>2</sub> and photon flux density. *Photosynthetica* 43:247–252. doi:10.1007/s11099-005-0040-z
- Atkin OK, Loveys BR, Atkinson LJ, Pons TL (2006a) Phenotypic plasticity and growth-temperature: understanding inter-specific variability. *J Exp Bot* 57:267–281. doi:10.1093/jxb/erj029
- Atkin OK, Scheurwater I, Pons TL (2006b) High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congeneric. *Glob Change Biol* 12:500–515. doi:10.1111/j.1365-2486.2006.01114.x
- Bernacchi CJ, Singaas EL, Pimentel C, Portis AR Jr, Long SP (2001) Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant Cell Environ* 24:253–259. doi:10.1111/j.1365-3040.2001.00668.x
- Berry J, Björkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annu Rev Plant Physiol* 31:491–543. doi:10.1146/annurev.pp.31.060180.002423
- Bertin N, Tchamitchian M, Baldet P, Devaux C, Brunel B, Gary C (1999) Contribution of carbohydrate pools to the variations in leaf mass per area within a tomato plant. *New Phytol* 143:53–61. doi:10.1046/j.1469-8137.1999.00436.x
- Bunce JA (2000) Acclimation of photosynthesis to temperature in eight cool and warm climate herbaceous C<sub>3</sub> species: temperature dependence of parameters of a biochemical photosynthesis model. *Photosynth Res* 63:59–67. doi:10.1023/A:1006325724086
- von Caemmerer S (2000) Biochemical models of leaf photosynthesis. CSIRO Publishing, Canberra
- Dreyer E, Le Roux X, Montpied P, Daudet FA, Masson F (2001) Temperature response of leaf photosynthetic capacity in seedlings from seven temperature tree species. *Tree Physiol* 21:223–232
- Ethier GJ, Livingston NJ (2004) On the need to incorporate sensitivity to CO<sub>2</sub> transfer conductance into the Farquhar-von Caemmerer-Berry leaf photosynthesis model. *Plant Cell Environ* 27:137–153. doi:10.1111/j.1365-3040.2004.01140.x
- Farquhar GD, von Caemmerer S (1982) Modelling of photosynthetic response to environmental conditions. In: Lange OL, Nobel PL, Osmon CB, Ziegler H (eds) *Encyclopedia of plant physiology*, NS. Physiological plant ecology II, vol 12 B. Springer, Berlin, pp 550–587
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149:78–90. doi:10.1007/BF00386231
- Ferrar PJ, Slatyer RO, Vranjic JA (1989) Photosynthetic temperature acclimation in *Eucalyptus* species from diverse habitats, and a comparison with *Nerium oleander*. *Aust J Plant Physiol* 16:199–217
- Ghouil H, Montpied P, Epron D, Ksontini M, Hanchi B, Dreyer E (2003) Thermal optima of photosynthetic functions and thermostability of photochemistry in cork oak seedlings. *Tree Physiol* 23:1031–1039
- Harley PC, Tenhunen JD (1991) Modeling the photosynthetic response of C<sub>3</sub> leaves to environmental factors. In: *Modeling crop photosynthesis—from biochemistry to canopy*, vol 19. American Society of Agronomy and Crop Science Society of America, Madison, pp 17–39
- Harley PC, Thomas RB, Reynolds JF, Strain BR (1992) Modelling photosynthesis of cotton grown in elevated CO<sub>2</sub>. *Plant Cell Environ* 15:271–282. doi:10.1111/j.1365-3040.1992.tb00974.x
- Hikosaka K, Hanba YT, Hirose T, Terashima I (1998) Photosynthetic nitrogen-use efficiency in woody and herbaceous plants. *Funct Ecol* 12:896–905. doi:10.1046/j.1365-2435.1998.00272.x
- Hikosaka K, Murakami A, Hirose T (1999) Balancing carboxylation and regeneration of ribulose-1,5-bisphosphate in leaf photosynthesis: temperature acclimation of an evergreen tree, *Quercus myrsinaefolia*. *Plant Cell Environ* 22:841–849. doi:10.1046/j.1365-3040.1999.00442.x
- Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y (2006) Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. *J Exp Bot* 57:291–302. doi:10.1093/jxb/erj049
- June T, Evans JR, Farquhar GD (2004) A simple new equation for the reversible temperature dependence of photosynthetic electron transport: a study on soybean leaf. *Funct Plant Biol* 31:275–283. doi:10.1071/FP03250
- Kattge J, Knorr W (2007) Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant Cell Environ* 30:1176–1190. doi:10.1111/j.1365-3040.2007.01690.x
- Le Roux X, Grand S, Dreyer E, Duadet FA (1999) Parameterization and testing of a biochemically based photosynthesis model for walnut (*Juglans regia*) trees and seedlings. *Tree Physiol* 19:181–188
- Leuning R (1997) Scaling to a common temperature improves the correlation between the photosynthesis parameters  $J_{max}$  and  $V_{cmax}$ . *J Exp Bot* 48:345–347. doi:10.1093/jxb/48.2.345
- Makino A, Nakano H, Mae T (1994) Effects of growth temperature on the response of ribulose-1,5-bisphosphate carboxylase, electron transport components, and sucrose synthesis enzymes to leaf nitrogen in rice, and their relationships to photosynthesis. *Plant Physiol* 105:1231–1238
- Mason N, Hughes P, McMullan R, Houghton JT (2001) Vegetation growth and the carbon balance. In: *Introduction to environmental physics: planet Earth, life and climate*. Taylor & Francis group, London, pp 363–396
- Mediavilla S, Escudero A, Heilmeyer H (2001) Internal leaf anatomy and photosynthetic resource-use efficiency: interspecific and intraspecific comparisons. *Tree Physiol* 21:251–259
- Medlyn BE, Dreyer E, Ellsworth D, Forstreuter M, Harley PC, Kirschbaum MUF et al (2002a) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant Cell Environ* 25:1167–1179. doi:10.1046/j.1365-3040.2002.00891.x

- Medlyn BE, Loustau D, Delzon S (2002b) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Ait.). *Plant Cell Environ* 25:1155–1165. doi:10.1046/j.1365-3040.2002.00890.x
- Niinemets Ü, Tenhunen JD (1997) A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade tolerant species *Acer saccharum*. *Plant Cell Environ* 20:845–856. doi:10.1046/j.1365-3040.1997.d01-133.x
- Niinemets Ü, Oja V, Kull O (1999a) Shape of leaf photosynthetic electron transport versus temperature response curve is not constant along canopy light gradients in temperate deciduous trees. *Plant Cell Environ* 22:1497–1513. doi:10.1046/j.1365-3040.1999.00510.x
- Niinemets Ü, Tenhunen JD, Canta NR, Chaves M, Faria T, Pereira JS et al (1999b) Interactive effects of nitrogen and phosphorus on the acclimation potential of foliage photosynthetic properties of cork oak, *Quercus suber*, to elevated CO<sub>2</sub> concentrations. *Glob Change Biol* 5:455–470. doi:10.1046/j.1365-2486.1999.00241.x
- Onoda Y, Hikosaka K, Hirose T (2005a) Seasonal change in the balance between capacities of RuBP carboxylation and RuBP regeneration affects CO<sub>2</sub> response of photosynthesis in *Polygonum cuspidatum*. *J Exp Bot* 56:755–763. doi:10.1093/jxb/eri052
- Onoda Y, Hikosaka K, Hirose T (2005b) The balance between RuBP carboxylation and RuBP regeneration: a mechanism underlying the interspecific variation in acclimation of photosynthesis to seasonal change in temperature. *Funct Plant Biol* 32:903–910. doi:10.1071/FP05024
- Raj S, Das G, Pothen J, Dey SK (2005) Relationship between latex yield of *Hevea brasiliensis* and antecedent environmental parameters. *Int J Biometeorol* 49:189–196. doi:10.1007/s00484-004-0222-6
- Rao PS, Saraswathyamma CK, Sethuraj MR (1998) Studies on the relationship between yield and meteorological parameters of para rubber tree (*Hevea brasiliensis*). *Agric For Meteorol* 90:235–245. doi:10.1016/S0168-1923(98)00051-3
- Robakowski P, Monpied P, Dreyer E (2002) Temperature response of photosynthesis of silver fir (*Abies alba* Mill.) seedlings. *Ann For Sci* 59:163–170. doi:10.1051/forest:2002003
- Sage RF, Kubien DS (2007) The temperature response of C<sub>3</sub> and C<sub>4</sub> photosynthesis. *Plant Cell Environ* 30:1086–1106. doi:10.1111/j.1365-3040.2007.01682.x
- Salvucci ME, Crafts-Brandner SJ (2004) Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. *Plant Physiol* 134:1460–1470. doi:10.1104/pp.103.038323
- Slatyer RO (1977a) Altitudinal variation in photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. III. Temperature response of material grown in contrasting thermal environments. *Aust J Plant Physiol* 4:301–312
- Slatyer RO (1977b) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. IV. Temperature response of four populations grown at different temperatures. *Aust J Plant Physiol* 4:583–594
- Slatyer RO, Morrow PA (1977) Altitudinal variation in photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. I. Seasonal changes under field conditions in the snowy mountains area of south-eastern Australia. *Aust J Plant Physiol* 25:1–20
- Takashima T, Hikosaka K, Hirose T (2004) Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. *Plant Cell Environ* 27:1047–1054. doi:10.1111/j.1365-3040.2004.01209.x
- Usami T, Lee J, Oikawa T (2001) Interactive effects of increased temperature and CO<sub>2</sub> on the growth of *Quercus myrsinaefolia* saplings. *Plant Cell Environ* 24:1007–1019. doi:10.1046/j.1365-3040.2001.00753.x
- Walcroft AS, Kelliher FM (1997) The response of photosynthetic model parameters to temperature and nitrogen concentration in *Pinus radiata* D. Don. *Plant Cell Environ* 20:1338–1348. doi:10.1046/j.1365-3040.1997.d01-31.x
- Warren CR (2008) Does growth temperature affect the temperature responses of photosynthesis and internal conductance to CO<sub>2</sub>? A test with *Eucalyptus regnans*. *Tree Physiol* 28:11–19
- Warren CR, Dreyer E (2006) Temperature response of photosynthesis and internal conductance to CO<sub>2</sub>: results from two independent approaches. *J Exp Bot* 57:3057–3067. doi:10.1093/jxb/erl067
- Wullschlegel SD (1993) Biochemical limitations to carbon assimilation in C<sub>3</sub> plants—a retrospective analysis of the A/C<sub>i</sub> curves from 109 species. *J Exp Bot* 44:907–920. doi:10.1093/jxb/44.5.907
- Yamasaki T, Yamakawa T, Yamane Y, Koike H, Satoh K, Katoh S (2002) Temperature acclimation of photosynthesis and related changes in photosystem II electron transport in winter wheat. *Plant Physiol* 128:1087–1097. doi:10.1104/pp.010919
- Yamori W, Nokuchi K, Terashima I (2005) Temperature acclimation of photosynthesis in spinach leaves: analyses of photosynthetic components and temperature dependencies of photosynthetic partial reactions. *Plant Cell Environ* 28:536–547. doi:10.1111/j.1365-3040.2004.01299.x
- Yamori W, Suzuki K, Noguchi K, Nakai M, Terashima I (2006) Effects of rubisco kinetics and rubisco activation state on the temperature dependence of the photosynthetic rate in spinach leaves from contrasting growth temperatures. *Plant Cell Environ* 29:1659–1670. doi:10.1111/j.1365-3040.2006.01550.x