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Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data

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ABSTRACT

The temperature dependence of C₃ photosynthesis is known to vary with growth environment and with species. In an attempt to quantify this variability, a commonly used biochemically based photosynthesis model was parameterized from 19 gas exchange studies on tree and crop species. The parameter values obtained described the shape and amplitude of the temperature responses of the maximum rate of Rubisco activity (V_{cmax}) and the potential rate of electron transport (J_{max}). Original data sets were used for this review, as it is shown that derived values of V_{cmax} and its temperature response depend strongly on assumptions made in derivation. Values of J_{max} and V_{cmax} at 25 °C varied considerably among species but were strongly correlated, with an average $J_{\text{max}} : V_{\text{cmax}}$ ratio of 1.67. Two species grown in cold climates, however, had lower ratios. In all studies, the $J_{\text{max}} : V_{\text{cmax}}$ ratio declined strongly with measurement temperature. The relative temperature responses of J_{max} and V_{cmax} were relatively constant among tree species. Activation energies averaged 50 kJ mol⁻¹ for J_{max} and 65 kJ mol⁻¹ for V_{cmax} , and for most species temperature optima averaged 33 °C for J_{max} and 40 °C for V_{cmax} . However, the cold climate tree species had low temperature optima for both J_{max} (19 °C) and V_{cmax} (29 °C), suggesting acclimation of both processes to growth temperature. Crop species had somewhat different temperature responses, with higher activation energies for both J_{max} and V_{cmax} , implying narrower peaks in the temperature response for these species. The results thus suggest that both growth environment and

plant type can influence the photosynthetic response to temperature. Based on these results, several suggestions are made to improve modelling of temperature responses.

Key-words: electron transport; model parameters; photosynthesis; ribulose-1,5-bisphosphate carboxylase-oxygenase; ribulose-1,5-bisphosphate regeneration; temperature acclimation.

INTRODUCTION

Many of the models used to study effects of global change on plant function and growth incorporate the Farquhar, von Caemmerer & Berry (1980) model of C₃ photosynthesis (e.g. Cramer *et al.* 2001). This model is particularly useful in this context because it represents mechanistically the effects of elevated atmospheric [CO₂], a major factor in global change, on photosynthesis. The model has two major parameters, the potential rate of electron transport (J_{max}) and the maximum rate of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) activity (V_{cmax}). There is now a large database of values of J_{max} and V_{cmax} (Wullschlegel 1993) and the effects of elevated [CO₂] on these parameters (Medlyn *et al.* 1999). The model also has the potential to accurately represent the effects of elevated temperature, a second major factor in global change that directly affects plant growth. However, as many modellers are aware, there is a dearth of information regarding the temperature responses of J_{max} and V_{cmax} (Leuning 1997).

We know that these temperature responses are likely to vary, because the temperature response of photosynthesis itself varies with genotype and environmental conditions, and may acclimate to changes in growth temperature (Slatyer & Morrow 1977; Berry & Björkman 1980). To date, however, there has been a fairly limited number of studies

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examining temperature responses in the context of the Farquhar model (Leuning 1997). The limited amount of information available can result in possibly inappropriate parameter choices. The database of temperature responses of model parameters has the potential to expand in the near future, given recent improvements in temperature control in commercially available gas exchange systems. However, there is a second obstacle to identifying variation in these responses between species, which is that parameter values obtained from data can differ according to the method used to derive them, as is shown below. Direct comparison of parameter values between different studies can therefore be misleading. Wullschleger (1993) solved this problem when compiling a database of J_{\max} and V_{\max} by deriving all parameter values himself directly from $A-C_i$ curves, thus ensuring consistency between parameters.

The aim of this study was to improve modelling of photosynthetic temperature responses by compiling and comparing existing information on the temperature response of the parameters of the Farquhar *et al.* (1980) model of photosynthesis. Few studies have compared variation of these parameters among species, so a broad understanding of temperature responses and their relationship to species characteristics and growth environment is lacking. We adopted the approach of Wullschleger (1993), using consistent methods to derive model parameters from the original data sets. Some 19 data sets were obtained. In order to draw some generalizations from these data sets, we attempted to link variation in the parameters between data sets to ecological factors such as functional type and growth environment.

METHODS

Data

Estimates of the parameters J_{\max} and V_{\max} may be obtained in several ways including gas exchange (Kirschbaum & Farquhar 1984; Harley, Tenhunen & Lange 1986), *in vitro* methods (Badger & Collatz 1977; Armond, Schreiber & Björkman 1978) or chlorophyll fluorescence (Niinemets, Oja & Kull 1999). In order to ensure that responses were comparable, we chose only to include gas exchange data. In this method, values of J_{\max} and V_{\max} are obtained from the response of photosynthesis under high light (A) to intercellular CO_2 (C_i). A family of $A-C_i$ curves at different temperatures will thus give the temperature response of the two parameters J_{\max} and V_{\max} . Obtaining such a family of curves is very time-consuming and hence several authors have attempted to estimate the temperature responses of J_{\max} and V_{\max} using reduced data sets (e.g. Hikosaka, Murakami & Hirose 1999; Wohlfahrt *et al.* 1999). We attempted to include some of these studies here, but we found that such shortcuts considerably reduced the accuracy of the parameter values, and therefore decided against their inclusion.

We required the original $A-C_i$ curves from each study, for reasons illustrated below. However, in two cases the

original data were no longer available (Kirschbaum & Farquhar 1984; Harley *et al.* 1992). Temperature responses from these two studies have been extensively used in modelling, so we thought it important to include them in the comparison. Therefore, in these two cases, typical $A-C_i$ curves were reconstructed from reported parameter values and the model was re-fitted to these curves. Statistical information on parameters obtained in this way is necessarily missing. Details of all data sets used are given in Table 1.

In most cases, temperature responses were obtained by applying temperature control to leaves for the duration of the gas exchange measurements. In contrast, in the experiments carried out by Dreyer *et al.* (2001) and Robakowski, Montpied & Dreyer (2002) (Table 1), temperature changes were applied to the whole seedlings for the night preceding the measurements. This procedure could potentially have modified the temperature response, as there is evidence that the thermal properties of photosystem II (PSII) and of electron transport may begin to acclimate after even a few hours at a given temperature (e.g. Havaux 1993). The results presented below, however, do not appear to indicate any difference between the experiments carried out by this group and other experiments.

Model

Overview of the Farquhar *et al.* (1980) model of photosynthesis

Farquhar *et al.* (1980) proposed that net leaf photosynthesis, A_n , could be modelled as the minimum of two limiting rates:

$$A_n = \min(A_c, A_j) - R_d \quad (1)$$

A_c is the rate of photosynthesis when Rubisco activity is limiting and A_j the rate when ribulose-1,5-bisphosphate (RuBP)-regeneration is limiting. R_d is the rate of mitochondrial respiration. Rubisco-limited photosynthesis is given by:

$$A_c = \frac{V_{\max}(C_i - \Gamma^*)}{\left[C_i + K_c \left(1 + \frac{O_i}{K_o} \right) \right]} \quad (2)$$

where V_{\max} is the maximum rate of Rubisco activity, C_i and O_i are the intercellular concentrations of CO_2 and O_2 , respectively, K_c and K_o are the Michaelis-Menten coefficients of Rubisco activity for CO_2 and O_2 , respectively, and Γ^* is the CO_2 compensation point in the absence of mitochondrial respiration. This formulation of the model assumes that the cell-wall conductance, the conductance between the intercellular space and the site of carboxylation, is negligible. Some authors have argued that this conductance is significant and may vary with leaf temperature (e.g. Makino, Nakano & Mae 1994). For most species considered here, we did not have access to appropriate data to evaluate the cell-wall conductance and hence were obliged to use the form of the model given above.

Table 1. Details of experimental data sets used

Species	Common name	Author	Measurement <i>T</i>	Plants	Points	Growth <i>T</i>	Growth conditions	Age of plants	Notes
Crops									
<i>Glycine max</i>	Soybean	Harley, Weber & Gates (1985)	20,25,30,35,40	3	48	25	GH – T	seedlings	O ₂ varied also
<i>Gossypium hirsutum</i>	Cotton	Harley <i>et al.</i> (1992)	18,26,29,35	2		29	GH – T	seedlings	Raw data unavailable
Deciduous trees									
<i>Acer pseudoplatanus</i>	Sycamore	Dreyer <i>et al.</i> (2001)	10,18,25,32,36,40	5	28	16	N (France)	seedlings	
<i>Betula pendula</i>	Silver birch	Wang (unpub.)	5,10,22,26,32	4	20	14	OTC (Finland)	seedlings	
<i>Betula pendula</i>	Silver birch	Dreyer <i>et al.</i> (2001)	10,18,25,32,40	5	25	17	N (France)	seedlings	
<i>Fagus sylvatica</i>	Common beech	Dreyer <i>et al.</i> (2001)	10,18,25,32,40	5	25	17	N (France)	seedlings	
<i>Fagus sylvatica</i>	Common beech	Strassemeyer & Forstreuter (1997)	19,23,26,30,35	7	28	20	ME (Germany)	seedlings	
<i>Fraxinus excelsior</i>	Ash	Dreyer <i>et al.</i> (2001)	10,18,25,32,36,40	5	30	16	N (France)	seedlings	
<i>Juglans regia</i>	Walnut	Dreyer <i>et al.</i> (2001)	10,18,25,32,40	5	25	17	N (France)	seedlings	
<i>Prunus persica</i>	Peach	Walcroft <i>et al.</i> (2002)	10,20,25,32,37	5	19	19	GH (France)	2 year	
<i>Quercus petraea</i>	Sessile oak	Dreyer <i>et al.</i> (2001)	10,18,25,32,36,40	5	25	16	N (France)	seedlings	
<i>Quercus robur</i>	English oak	Dreyer <i>et al.</i> (2001)	10,18,25,32,36,40	5	30	16	N (France)	seedlings	
<i>Quercus robur</i>	English oak	Strassemeyer & Forstreuter (unpub.)	15,21,26,30,36	8	29	20	ME (Germany)	seedlings	
Evergreen trees									
<i>Abies alba</i>	Silver fir	Robakowski <i>et al.</i> (2002)	10,18,26,32,36,40	5	28	25	N (France)	seedlings	
<i>Eucalyptus pauciflora</i>	Snowgum	Kirschbaum & Farquhar (1984)	15–35	1		20	GH – T	seedlings	Raw data unavailable
<i>Pinus pinaster</i>	Maritime pine	Medlyn <i>et al.</i> (2002)	15,20,25,30,35	6	27	24	field (France)	30 year	Local provenance, August
<i>Pinus radiata</i>	Radiata pine	Walcroft <i>et al.</i> (1997)	8,15,20,25,30	3	14	24	GH (NZ)	seedlings	Two fertilization treatments
<i>Pinus sylvestris</i>	Scots pine	Wang, Kellomaki & Laitinen (1996)	6,11,21,26,31	4	18	14	OTC (Finland)	20–25 year	
<i>Pinus taeda</i>	Loblolly pine	Ellsworth & Klimas (submitted)	15,28,35	5	14	24	FACE (N. Carolina)	12 year	June and August combined

Points is the total number of data points used. Growth *T* is the mean temperature in the month preceding the measurements. Growth conditions: GH, greenhouse; GH – T, temperature-controlled greenhouse; N, nursery; OTC, open-top chamber (control treatment); ME, mini-ecosystem (control treatment); FACE, free-air CO₂ exchange (control ring).

The rate of photosynthesis when RuBP regeneration is limiting is given by:

$$A_j = \left(\frac{J}{4}\right) \times \frac{(C_i - \Gamma^*)}{(C_i + 2\Gamma^*)} \quad (3)$$

where J is the rate of electron transport. J is related to incident photosynthetically active photon flux density, Q , by:

$$\theta J^2 - (\alpha Q + J_{\max})J + \alpha Q J_{\max} = 0 \quad (4)$$

where J_{\max} is the potential rate of electron transport, θ is the curvature of the light response curve and α is the quantum yield of electron transport. The value of α was fixed at 0.3 mol electrons mol⁻¹ photon, based on an average C₃ photosynthetic quantum yield of 0.093 and a leaf absorptance of 0.8 (Long, Postl & Bolharnordenkamp 1993). The value of θ was taken to be 0.90. These parameter values have only a slight effect on the estimated value of J_{\max} .

The key parameters of the model, which vary among species, are J_{\max} and V_{\max} . It is the temperature dependences of these parameters that we set out to examine. In addition, it is known that the parameters K_c , K_o and Γ^* vary with temperature. These parameters, by contrast, are thought to be intrinsic properties of the Rubisco enzyme and are generally assumed constant among species, thereby minimizing the number of parameters to be fitted (Harley *et al.* 1986).

*T-dependence of K_c , K_o , and Γ^**

The *in-vivo* temperature dependence of the Michaelis-Menten coefficients of Rubisco, K_c ($\mu\text{mol mol}^{-1}$) and K_o (mmol mol^{-1}), was recently measured in transgenic tobacco over the temperature range 10–40 °C (Bernacchi *et al.* 2001) and the following relationships obtained:

$$K_c = 404.9 \exp\left[\frac{79430(T_k - 298)}{(298RT_k)}\right] \quad (5)$$

$$K_o = 278.4 \exp\left[\frac{36380(T_k - 298)}{(298RT_k)}\right] \quad (6)$$

T_k denotes leaf temperature in K and R is the universal gas constant (8.314 J mol⁻¹ K⁻¹). Previous parameterizations of the photosynthesis model have been based on *in vitro* determinations of these functions, carried out by Badger & Collatz (1977) and Jordan & Ogren (1984), which are given here for comparison. Badger & Collatz (1977) determined carboxylase and oxygenase activities over the temperature range 5–35 °C of Rubisco purified from leaves of *Atriplex glabriscula*. They obtained the following relations (as given in Farquhar *et al.* 1980):

$$K_c = 460 \exp\left[\frac{59536(T_k - 298)}{(298RT_k)}\right] \quad (T > 15^\circ\text{C}) \quad (7)$$

$$= 920 \exp\left[\frac{109700(T_k - 298)}{(298RT_k)}\right] \quad (T < 15^\circ\text{C}) \quad (8)$$

$$K_o = 330 \exp\left[\frac{35948(T_k - 298)}{(298RT_k)}\right] \quad (9)$$

Jordan & Ogren (1984), working with Rubisco purified from spinach over the temperature range 5–40 °C, obtained the following relationships (equations derived by Harley & Baldocchi 1995):

$$K_c = 274.6 \exp\left[\frac{80500(T_k - 298)}{(298RT_k)}\right] \quad (10)$$

$$K_o = 419.8 \exp\left[\frac{14500(T_k - 298)}{(298RT_k)}\right] \quad (11)$$

Figure 1a illustrates the temperature dependence of the effective Michaelis-Menten coefficient for CO₂, $K_m = K_c(1 + O_i/K_o)$, at an intercellular O₂ concentration of 210 mmol mol⁻¹, using each of these three sets of equations.

Similarly, the temperature dependence of the CO₂ compensation point, Γ^* ($\mu\text{mol mol}^{-1}$), was estimated by Bernacchi *et al.* (2001) to be:

$$\Gamma^* = 42.75 \exp\left[\frac{37830(T_k - 298)}{(298RT_k)}\right] \quad (12)$$

Alternative expressions of the temperature dependence of the CO₂ compensation point, Γ^* , are generally based on the work of either Badger and colleagues (Badger & Andrews 1974, Badger & Collatz 1977), Jordan & Ogren (1984) or Brooks & Farquhar (1985). These three alternative temperature dependences are illustrated in Fig. 1b. The CO₂ compensation point is related to K_c and K_o and to the maximum oxygenation activity of Rubisco, V_{\max} (Farquhar *et al.* 1980):

$$\Gamma^* = \frac{K_c V_{\max} O_i}{(2K_o V_{\max})} \quad (13)$$

Badger & Andrews (1974) observed that the ratio $V_{\max}/V_{\max} = 0.21$, independent of temperature, allowing the temperature dependence of Γ^* to be determined from that of K_c and K_o . Jordan & Ogren (1984) studied the CO₂ specificity factor $\tau = K_c V_{\max}/(K_o V_{\max})$ of Rubisco purified from spinach and obtained (equation derived by Harley *et al.* 1992):

$$\tau = 2.321 \exp\left[-\frac{29000(T_k - 298)}{(298RT_k)}\right] \quad (14)$$

Brooks & Farquhar (1985) estimated the CO₂ compensation point of spinach *in vivo* using a gas-exchange technique and obtained the following relation, valid over the range 15–30 °C:

$$\Gamma^* = 42.7 + 1.68(T_k - 298) + 0.0012(T_k - 298)^2 \quad (15)$$

They report that this relationship closely resembles that obtained by Jordan & Ogren (1984).

We explored the significance of the differences between these alternative formulations when fitting the parameters J_{\max} and V_{\max} . We found that the parameter J_{\max} was only very slightly sensitive to the formulation of either K_m or Γ^* (not shown). However, the parameter V_{\max} was highly sensitive to the formulation of K_m chosen (Fig. 1c). The ratio of $J_{\max} \cdot V_{\max}$ was thus also highly sensitive to K_m (Fig. 1d). This sensitivity is the reason why we considered it necessary to

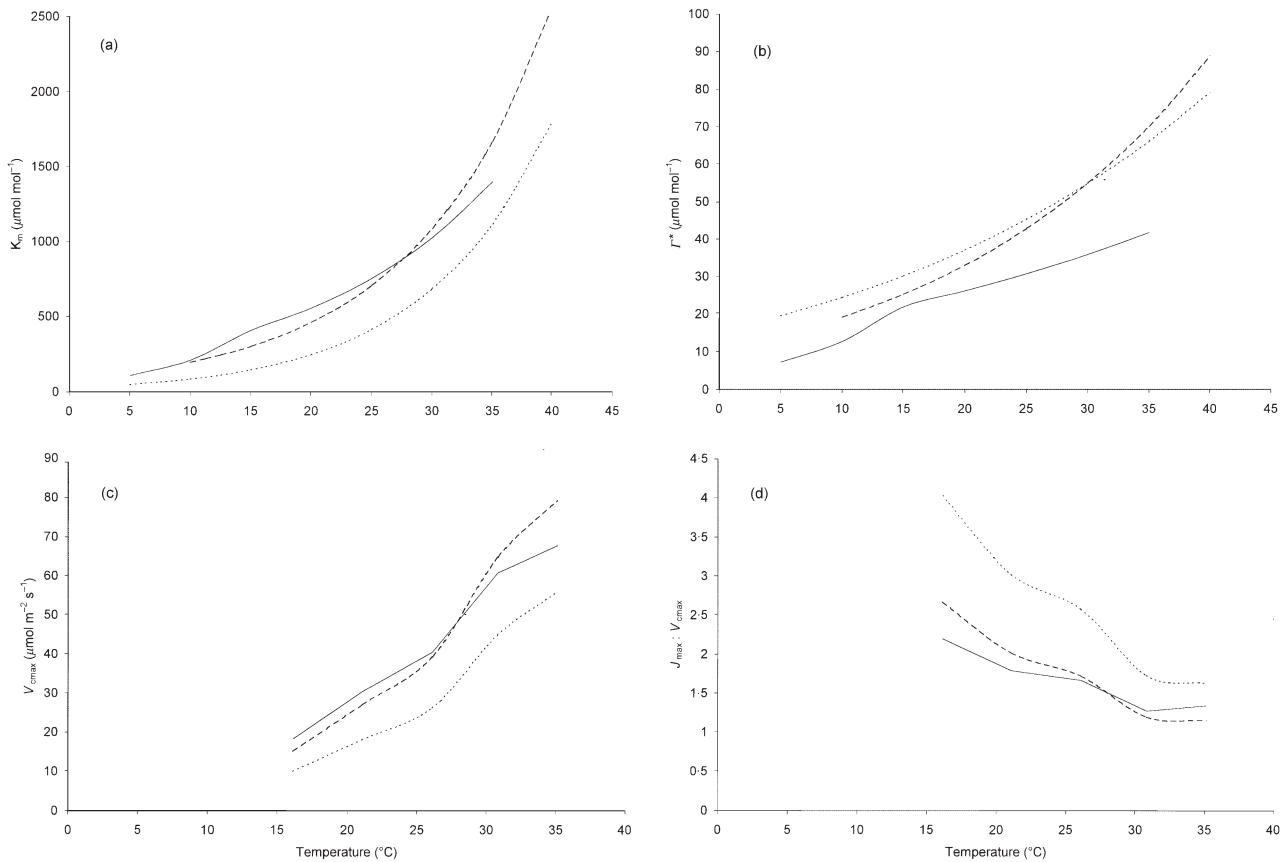


Figure 1. (a) Alternative forms for the response of $K_m = K_c(1 + O_i/K_o)$ to leaf temperature. (b) Alternative forms for the response of Γ^* to leaf temperature. (c) Response of V_{cmax} to leaf temperature obtained by fitting a sample data set using alternative forms for K_m . (d) Response of ratio $J_{max} : V_{cmax}$ to leaf temperature obtained by fitting a sample data set using alternative forms for K_m . Key: Solid line: data from Badger & Collatz (1977). Dotted line: data from Jordan & Ogren (1984). Dashed line: data from Bernacchi *et al.* (2001).

use a consistent method to derive all parameters in a consistent fashion from original $A-C_i$ curves before comparing the temperature responses.

In the current work, we chose to use the temperature functions obtained by Bernacchi *et al.* (2001), because these functions were measured *in vivo*, without disturbance of the leaf, and are hence more likely to reflect accurately activity within the leaf. When using the temperature dependences of J_{max} and V_{cmax} presented below, it is important to also use the Bernacchi *et al.* (2001) temperature dependences for K_c , K_o and Γ^* , because of the sensitivity of the model to these functions illustrated in Fig. 1.

T-dependence of J_{max} and V_{cmax}

On reviewing the literature, it is daunting to observe the number of alternative functions that have been used to model the temperature dependences of J_{max} and V_{cmax} (compare, for example, Harley *et al.* 1986; Long 1991; Harley *et al.* 1992; Harley & Baldocchi 1995; Lloyd *et al.* 1995). However, all these equations are actually just alternative expressions of two basic functions. The first is the Arrhenius function:

$$f(T_k) = k_{25} \exp\left[\frac{E_a(T_k - 298)}{(298RT_k)}\right] \quad (16)$$

which has parameters k_{25} (the value at 25 °C) and E_a (the exponential rate of rise of the function). The second is a peaked function (Johnson, Eyring & Williams 1942), which is essentially the Arrhenius equation (Eqn 16) modified by a term that describes how conformational changes in the enzyme at higher temperatures start to negate the on-going benefits that would otherwise come from further increasing temperature. This equation can be written in two equivalent forms:

$$f(T_k) = k_{25} \exp\left[\frac{E_a(T_k - 298)}{(298RT_k)}\right] \frac{1 + \exp\left(\frac{298\Delta S - H_d}{298R}\right)}{1 + \exp\left(\frac{T_k\Delta S - H_d}{T_k R}\right)} \quad (17)$$

$$\text{or } f(T_k) = k_{opt} \frac{H_d \exp\left(\frac{H_a(T_k - T_{opt})}{T_k R T_{opt}}\right)}{H_d - H_a \left(1 - \exp\left(\frac{H_d(T_k - T_{opt})}{T_k R T_{opt}}\right)\right)} \quad (18)$$

The first form has parameters k_{25} , H_a , H_d and ΔS , whereas the second form has parameters k_{opt} , H_a , H_d and T_{opt} . H_a and H_d are the same between the two forms, whereas ΔS and T_{opt} are related by:

$$T_{opt} = \frac{H_d}{\Delta S - R \ln \left[\frac{H_a}{(H_d - H_a)} \right]} \quad (19)$$

The parameters can be interpreted as follows: k_{25} and k_{opt} are the values of J_{max} or V_{cmax} at temperatures 25 °C and T_{opt} , respectively; H_a gives the rate of exponential increase of the function below the optimum (and is analogous to parameter E_a in the Arrhenius function); H_d describes the rate of decrease of the function above the optimum; and T_{opt} is the optimum temperature. ΔS is known as an entropy factor but is not readily interpreted.

Model fitting

The first step in fitting the model was to obtain a value of J_{max} and V_{cmax} for each individual $A-C_i$ curve. This step was carried out by fitting Eqns 1, 2, 3 and 4 to each curve using the non-linear regression routine with Gaussian algorithm in SAS (SAS Institute Inc., Cary, NC, USA). The parameter R_d was also fitted but was not used further, because this parameter was found to be poorly estimated by the model.

Temperature response parameters were then obtained by fitting Eqns 16, 17 and 18 to response curves of J_{max} and V_{cmax} to leaf temperature, using SigmaPlot (SPSS Inc. Chicago, IL, USA). It was assumed that J_{max} and V_{cmax} at a given temperature could vary between leaves (according to factors such as leaf nitrogen per unit area) but that relative temperature responses of the parameters would be constant. This assumption was incorporated in the model by introducing dummy variables l_i to represent each leaf and putting:

$$k = \sum_i l_i k_i \quad (20)$$

in Eqns 16, 17 and 18 (Kleinbaum *et al.* 1998). Here, $l_i = 1$ for leaf i and 0 otherwise, and k_i is the value of k_{25} or k_{opt} for leaf i . Reported values of the parameters k_{25} and k_{opt} are mean and standard deviation of values of k_i .

The Arrhenius model is a subset of the peaked model (compare Eqns 16 and 17). Therefore, an F -test was used to determine whether the peaked model gave a significantly better fit to data than the Arrhenius model (Kleinbaum *et al.* 1998). As others have found, the four-parameter peaked model was often over-parameterized, i.e. there was insufficient data to determine all parameters (Harley *et al.* 1992; Dreyer *et al.* 2001). Hence, this model was also fitted under the assumption that $H_d = 200$ kJ mol⁻¹, and an F -test used to determine whether H_d was significantly different from this value.

Implied temperature response of photosynthesis

We wanted to identify the implications for photosynthesis of differences in the temperature responses of model

parameters. To do so, Eqns 1, 2, 3 and 4 were used to calculate a typical temperature response of net photosynthesis from the derived parameter values. This calculation was made by assuming standard ambient environmental conditions for light-saturated photosynthesis: an atmospheric [CO₂] concentration of 350 μmol mol⁻¹, a constant $C_i:C_a$ ratio of 0.7, and a value for J of 0.9 J_{max} . Leaf respiration was modelled for all species using a base rate of 0.01 V_{cmax} and a Q_{10} of 2.

RESULTS

Temperature response of V_{cmax}

Fitted parameters of the temperature response of V_{cmax} are given in Table 2. In most cases, the peaked function (Eqn 17) with H_d fixed at 200 kJ mol⁻¹ gave a significantly better fit to the data than the Arrhenius function (Eqn 16). In no case, however, did relaxing the constraint on H_d significantly improve the fit to the data. Species for which no peak in the temperature response of V_{cmax} was discernible were *Fraxinus excelsior*, *Prunus persica*, *Pinus taeda* and *Pinus radiata*. Note, however, that measurements on *P. radiata* did not go above 30 °C (Table 1), and that peak values close to 40 °C (maximal measurement temperature) are statistically difficult to estimate (e.g. for *F. excelsior*); in all cases a peak may well occur above the highest measurement temperature.

Values of k_{25} , the maximum rate of Rubisco activity at 25 °C, varied across data sets by a factor of three. Some of this variation is probably caused by variations in leaf nitrogen content between data sets. Values were highest for crop species, but were comparable for coniferous and deciduous species. Note that all rates are expressed on a one-sided leaf area basis.

The activation energy H_a was generally in the range 60–80 kJ mol⁻¹, implying a similarity in the temperature responses of V_{cmax} across data sets. Two data sets had values of H_a slightly below this range (*F. excelsior* and fertilized *P. radiata*) whereas another two had values of H_a considerably above this range (*Gossypium hirsutum* and *Juglans regia*).

The optimum temperature for V_{cmax} , T_{opt} , was undetermined for those experiments where the peaked function was not a significantly better fit than the Arrhenius function. Among the other experiments, T_{opt} was generally in the range 35–41 °C, with no clear pattern in the variation, with two exceptions. *Betula pendula* and *Pinus sylvestris*, grown in Finland, experienced the lowest growing temperatures and showed significantly lower values of T_{opt} (27–29 °C).

The variability in the temperature response of V_{cmax} is illustrated in Fig. 2a, which shows the temperature responses normalized to 1 at 25 °C. Most of the temperature responses lie between the two curves shown for *Juglans regia* and *Acer pseudoplatanus*. The exceptions are cotton, *Gossypium hirsutum*, which has a much steeper V_{cmax} - T response owing to its high value of H_a , and the

Table 2. Parameters of the temperature response of V_{cmax}

Species	Arrhenius model			Peaked model			r^2	T_{opt} (°C)	H_D (kJ mol ⁻¹)	H_A (kJ mol ⁻¹)	k_{opt} (μmol m ⁻² s ⁻¹)	k_{25} (μmol m ⁻² s ⁻¹)	E_a (kJ mol ⁻¹)	r^2	P
	k_{25} (μmol m ⁻² s ⁻¹)	E_a (kJ mol ⁻¹)	r^2	k_{25} (μmol m ⁻² s ⁻¹)	H_A (kJ mol ⁻¹)	H_D (kJ mol ⁻¹)									
Crops															
<i>Glycine max</i>	97.76 (9.15)	54.08 (3.86)	0.87	93.89 (8.34)	69.50 (24.37)	200.00	277.50 (24.66)	41.89 (9.92)	200.00	69.50 (24.37)	200.00	277.50 (24.66)	41.89 (9.92)	0.88	0.05
<i>Gossypium hirsutum</i>	91.48	93.59 (4.50)	1.00	90.22	116.38	200.00	399.26	40.60	200.00	116.38	200.00	399.26	40.60	1.00	
Deciduous trees															
<i>Acer pseudoplatanus</i>	72.96 (8.66)	33.92 (7.19)	0.66	78.16 (11.01)	75.88 (23.93)	200.00	136.28 (19.20)	34.95 (1.21)	200.00	75.88 (23.93)	200.00	136.28 (19.20)	34.95 (1.21)	0.86	0.00
<i>Betula pendula</i> OTC	85.07 (3.65)	37.19 (4.98)	0.87	101.90 (3.85)	63.75 (11.44)	200.00	114.82 (4.34)	29.28 (0.59)	200.00	63.75 (11.44)	200.00	114.82 (4.34)	29.28 (0.59)	0.97	0.00
<i>Betula pendula</i> GH	68.85 (14.19)	50.60 (3.86)	0.94	69.09 (14.72)	77.02 (18.76)	200.00	177.31 (37.78)	39.20 (3.76)	200.00	77.02 (18.76)	200.00	177.31 (37.78)	39.20 (3.76)	0.97	0.00
<i>Fagus sylvatica</i> GH	60.95 (5.48)	41.38 (4.31)	0.89	63.83 (5.17)	72.36 (15.34)	200.00	133.13 (10.78)	37.36 (0.87)	200.00	72.36 (15.34)	200.00	133.13 (10.78)	37.36 (0.87)	0.97	0.00
<i>Fagus sylvatica</i> ME	27.21 (3.41)	46.81 (3.53)	0.92	27.51 (2.93)	65.40 (19.48)	200.00	49.25 (5.24)	36.16 (3.63)	200.00	65.40 (19.48)	200.00	49.25 (5.24)	36.16 (3.63)	0.95	0.00
<i>Fraxinus excelsior</i>	77.97 (9.65)	50.61 (3.60)	0.93	78.43 (9.60)	54.58 (13.11)	200.00	235.89 (28.88)	45.52 (36.87)	200.00	54.58 (13.11)	200.00	235.89 (28.88)	45.52 (36.87)	0.93	0.47
<i>Juglans regia</i>	62.10 (10.24)	43.98 (6.21)	0.83	63.98 (10.62)	104.58 (23.56)	200.00	146.39 (24.30)	36.05 (0.45)	200.00	104.58 (23.56)	200.00	146.39 (24.30)	36.05 (0.45)	0.97	0.00
<i>Prunus persica</i>	65.50 (3.88)	73.74 (3.28)	0.99	66.16 (3.91)	75.14 (23.38)	200.00	464.59 (27.49)	50.86 (396.99)	200.00	75.14 (23.38)	200.00	464.59 (27.49)	50.86 (396.99)	0.99	1.00
<i>Quercus petraea</i>	79.50 (8.55)	56.28 (2.79)	0.98	79.11 (8.10)	67.72 (9.40)	200.00	244.53 (25.04)	42.77 (6.96)	200.00	67.72 (9.40)	200.00	244.53 (25.04)	42.77 (6.96)	0.99	0.01
<i>Quercus robur</i> GH	89.99 (11.98)	55.50 (3.45)	0.96	89.71 (11.92)	61.77 (13.57)	200.00	295.01 (39.19)	44.87 (25.44)	200.00	61.77 (13.57)	200.00	295.01 (39.19)	44.87 (25.44)	0.96	0.26
<i>Quercus robur</i> ME	40.83 (12.28)	46.26 (3.11)	0.97	42.32 (13.42)	57.59 (12.22)	200.00	84.97 (26.94)	38.76 (10.69)	200.00	57.59 (12.22)	200.00	84.97 (26.94)	38.76 (10.69)	0.97	0.06
Evergreen trees															
<i>Abies alba</i>	41.64 (5.15)	35.16 (3.97)	0.86	43.50 (5.33)	60.02 (9.88)	200.00	78.11 (9.56)	36.81 (0.65)	200.00	60.02 (9.88)	200.00	78.11 (9.56)	36.81 (0.65)	0.95	0.00
<i>Eucalyptus pauciflora</i>	87.73	51.56 (2.09)	0.99	90.42	60.79 (4.93)	200.00	175.81	37.83 (3.54)	200.00	60.79 (4.93)	200.00	175.81	37.83 (3.54)	1.00	
<i>Pinus pinaster</i>	89.98 (5.01)	62.22 (2.76)	0.99	92.42 (4.65)	74.16 (11.17)	200.00	213.30 (10.77)	38.34 (7.36)	200.00	74.16 (11.17)	200.00	213.30 (10.77)	38.34 (7.36)	0.99	0.01
<i>Pinus radiata</i> fert.	97.01 (4.46)	49.07 (3.73)	0.96	99.15 (4.71)	51.32 (19.21)	200.00	174.33 (8.33)	37.74 (152.04)	200.00	51.32 (19.21)	200.00	174.33 (8.33)	37.74 (152.04)	0.96	0.77
<i>Pinus radiata</i> unfert.	83.57 (17.5)	61.31 (3.71)	0.98	85.86 (17.7)	64.78 (21.32)	200.00	171.59 (35.81)	37.68 (125.99)	200.00	64.78 (21.32)	200.00	171.59 (35.81)	37.68 (125.99)	0.98	0.69
<i>Pinus sylvestris</i>	53.99 (7.22)	35.53 (5.93)	0.81	67.33 (9.72)	69.83 (12.56)	200.00	70.75 (10.21)	27.56 (0.61)	200.00	69.83 (12.56)	200.00	70.75 (10.21)	27.56 (0.61)	0.96	0.00
<i>Pinus taeda</i>	57.05 (9.33)	60.88 (3.68)	0.98	57.66 (9.43)	61.21 (304.11)	200.00	340.45 (55.63)	53.30 (47033)	200.00	61.21 (304.11)	200.00	340.45 (55.63)	53.30 (47033)	0.98	1.00

Values of k_{25} and k_{opt} are expressed on a one-sided leaf area basis. Standard deviations of k_{25} and k_{opt} , and standard errors of other parameters, are given in parentheses. P , probability that the peaked model is not a significantly better fit to the data than the Arrhenius model. OTC, open top chamber experiment; GH, greenhouse experiment; ME, mini-ecosystem experiment.

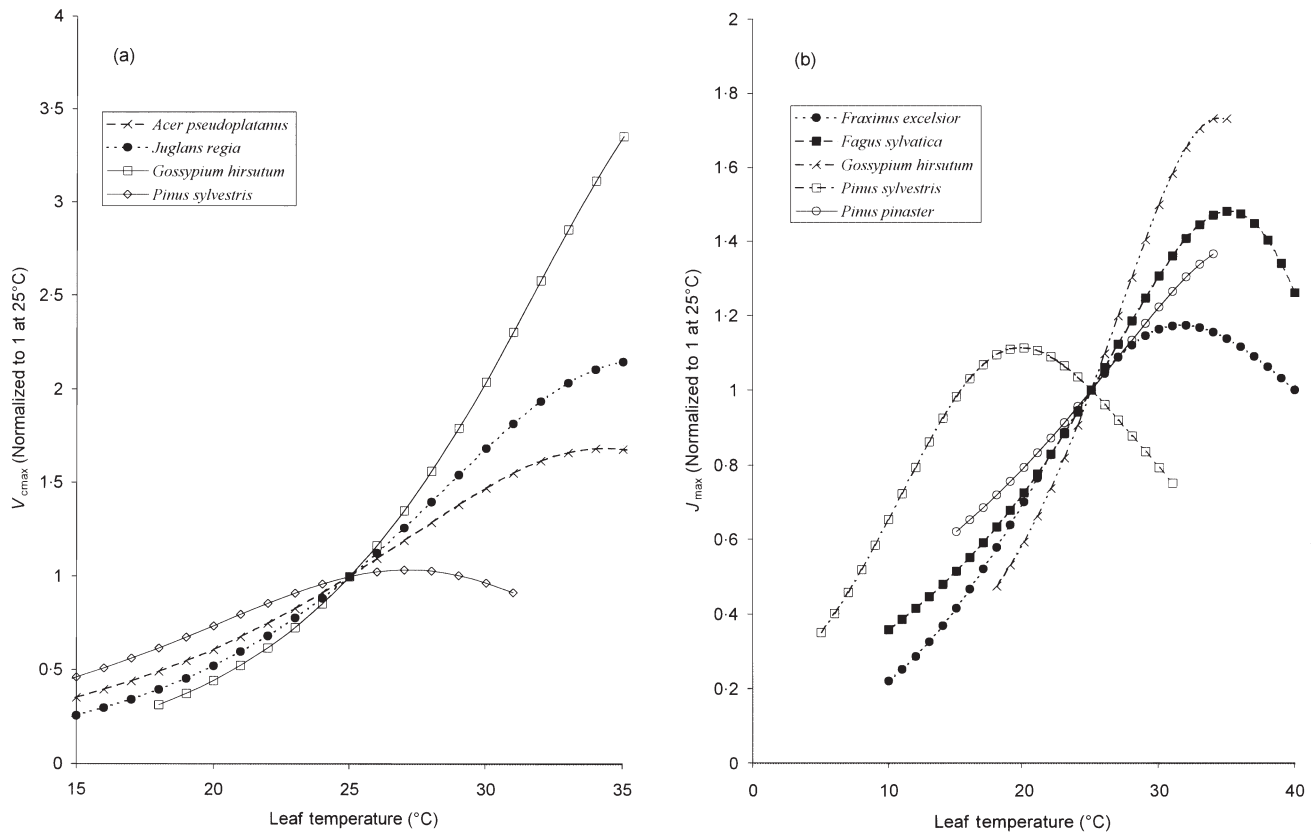


Figure 2. Sample responses of (a) V_{cmax} and (b) J_{max} to leaf temperature. Values are normalized to 1 at 25°C.

Finnish plants, *B. pendula* and *P. sylvestris*, which have a much lower optimal temperature for V_{cmax} .

Temperature response of J_{max}

The peaked function (Eqn 17) described the temperature response of J_{max} significantly better than the Arrhenius function (Eqn 16) for all experiments other than *P. radiata* and *P. taeda*. Parameters for the peaked function are given in Table 3.

Values of the activation energy H_a were in general highest for crop species (80–90 kJ mol⁻¹), intermediate for deciduous species (40–60 kJ mol⁻¹) and lowest for coniferous species (30–40 kJ mol⁻¹). The major exceptions to this pattern were again the cold-climate trees from Finland, *B. pendula* and *P. sylvestris*, which both had high values of H_a , and *F. excelsior*. Values of H_d were significantly less than 200 kJ mol⁻¹ for these three species and for soybean.

The optimal temperature for J_{max} is generally in the range 30–38°C, with no clear pattern among species, with the exception again of the Finnish plants. *Betula pendula* and *P. sylvestris* had much lower optimal temperatures for J_{max} of about 20°C.

The variability in the temperature response of J_{max} is illustrated in Fig. 2b. The two Finnish species have similar responses, with low optimal temperatures. The other conifers have responses resembling that of *P. pinaster*, with a

relatively low slope owing to low values of H_a . Deciduous tree responses generally lie between those of *F. excelsior* and *F. sylvatica*. Crop species responses are steeper again, as illustrated by the *G. hirsutum* response.

Ratio of $J_{max} : V_{cmax}$

Figure 3 shows the relationship between values of J_{max} and V_{cmax} at 25°C. Most of the data points fall close to a straight line with a slope of 1.67. The major exceptions to this pattern are soybean, with a ratio of 2.4, and the two Finnish plants, which both have ratios of about 1. For each experiment, a linear function was fitted to the relationship between the $J_{max} : V_{cmax}$ ratio and leaf temperature. There was a significant negative slope in all cases, ranging from –0.045 to –0.08, highlighting the difference in activation energies for J_{max} and V_{cmax} .

Implications for the temperature response of light-saturated photosynthesis

The temperature response of photosynthesis was modelled for each data set, under the assumption of a constant $C_i : C_a$ ratio. From the resulting curves, the optimal temperature for photosynthesis and its rate of increase over the range 15–30°C were calculated, and these are plotted in Figs 4 and 5 against growth temperature. Figure 4 illustrates that

Table 3. Parameters of the temperature response of J_{\max}

Species	$k_{25}(\mu\text{mol m}^{-2} \text{s}^{-1})$	$k_{\text{opt}}(\mu\text{mol m}^{-2} \text{s}^{-1})$	$H_a(\text{kJ mol}^{-1})$	$H_d(\text{kJ mol}^{-1})$	$T_{\text{opt}}(^{\circ}\text{C})$	r^2
Crops						
<i>Glycine max</i>	217.88 (2.89)	328.57 (4.35)	88.82 (36.57)	113.77 (10.78)	38.17 (2.33)	0.89
<i>Gossypium hirsutum</i>	131.82	221.57	77.17	200	34.44	1.00
Deciduous trees						
<i>Acer pseudoplatanus</i>	142.23 (12.37)	173.90 (15.12)	44.14 (10.02)	200	31.96 (1.16)	0.82
<i>Betula pendula</i> OTC	111.89 (1.48)	128.45 (1.70)	108.45 (18.29)	156.84 (12.60)	19.20 (0.70)	0.96
<i>Betula pendula</i> GH	116.33 (13.21)	169.66 (19.27)	42.83 (4.09)	200	35.77 (0.41)	0.98
<i>Fagus sylvatica</i> GH	97.91 (12.31)	173.18 (18.20)	48.09 (7.86)	200	35.24 (0.78)	0.95
<i>Fagus sylvatica</i> ME	44.83 (7.50)	51.89 (8.68)	43.36 (12.37)	200	30.78 (0.65)	0.94
<i>Fraxinus excelsior</i>	147.03 (18.51)	170.10 (21.42)	91.20 (15.20)	131.89 (7.58)	31.38 (0.62)	0.95
<i>Juglans regia</i>	103.81 (16.75)	165.86 (26.76)	56.30 (8.59)	200	35.53 (0.60)	0.97
<i>Prunus persica</i>	106.27 (7.83)	154.81 (11.41)	42.04 (8.73)	200	35.87 (1.56)	0.95
<i>Quercus petraea</i>	144.01 (12.02)	220.75 (18.43)	42.14 (2.99)	200	36.89 (0.34)	0.99
<i>Quercus robur</i> GH	139.59 (23.98)	212.90 (36.57)	36.92 (7.19)	200	37.91 (1.29)	0.92
<i>Quercus robur</i> ME	66.03 (20.18)	80.75 (24.68)	35.87 (13.52)	200	32.86 (1.19)	0.89
Evergreen trees						
<i>Abies alba</i>	95.49 (5.73)	128.15 (7.69)	50.82 (8.20)	200	33.20 (0.78)	0.90
<i>Eucalyptus pauciflora</i>	141.94	175.13	43.79	200	32.19	
<i>Pinus pinaster</i>	154.74 (10.80)	220.91 (15.40)	34.83 (9.24)	200	36.87 (9.34)	0.97
<i>Pinus radiata</i> fert.	175.43 (14.29)	189.66 (15.46)	43.18 (12.41)	200	29.01 (2.76)	0.95
<i>Pinus radiata</i> unfert.	136.57 (17.66)	145.99 (18.85)	44.14 (16.60)	200	28.63 (3.21)	0.92
<i>Pinus sylvestris</i>	70.77 (2.65)	78.36 (2.93)	100.28 (17.76)	147.92 (10.28)	19.89 (0.73)	0.96
<i>Pinus taeda</i>	98.54 (14.09)	155.76 (22.26)	37.87 (394.31)	200	38.48 (1213)	0.95

Values of k_{25} and k_{opt} are expressed on a one-sided leaf area basis. Standard deviations of k_{25} and k_{opt} , and standard errors of other parameters, are given in parentheses. OTC, open top chamber experiment; GH, greenhouse experiment; ME, mini-ecosystem experiment.

for the majority of broadleaf and coniferous trees, the optimal temperature for photosynthesis varies between 23 and 30 °C and is largely unrelated to growth temperature. However, the trees grown in cold conditions in Finland had considerably lower optimal temperatures. The optimal temperatures for the two crop species, which were grown in warm conditions, were comparable to the highest optimal temperatures obtained for the tree species. The rate of

increase of photosynthesis between 15 and 30 °C was also similar for most plants in the survey, ranging from 1.2 to 1.6 (Fig. 5). The exceptions were the Finnish trees, again, for which photosynthesis actually decreased over this temperature range, and walnut (*J. regia*) and cotton (*G. hirsutum*), which had particularly high rates of increase. From Figs 4 and 5 we can identify three broad classes of implied photosynthetic temperature response (Fig. 6). Most plants had

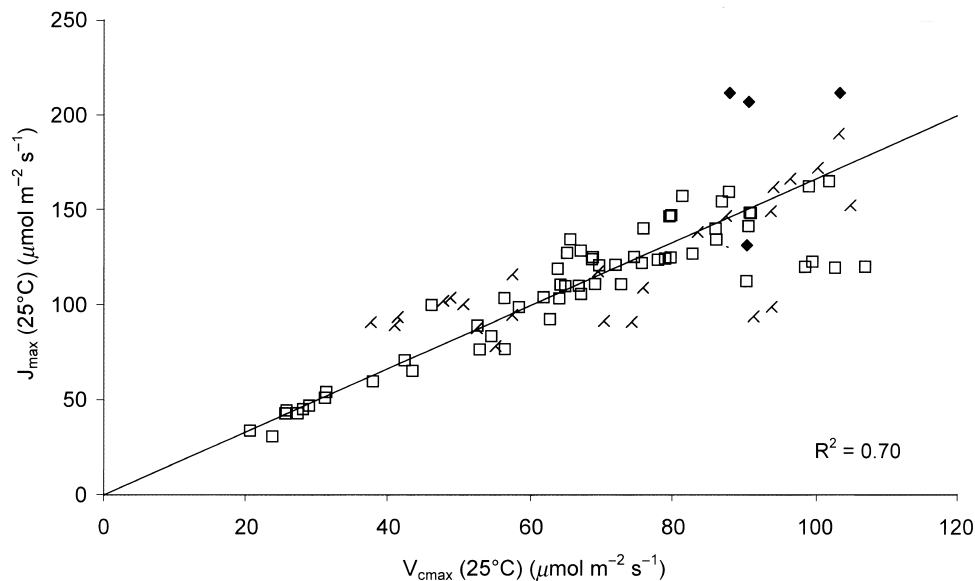


Figure 3. Relationship between J_{\max} and V_{cmax} at 25 °C. Filled symbols: crop species; open symbols: broadleaf species; crosses: coniferous species. Fitted regression line has slope of 1.67.

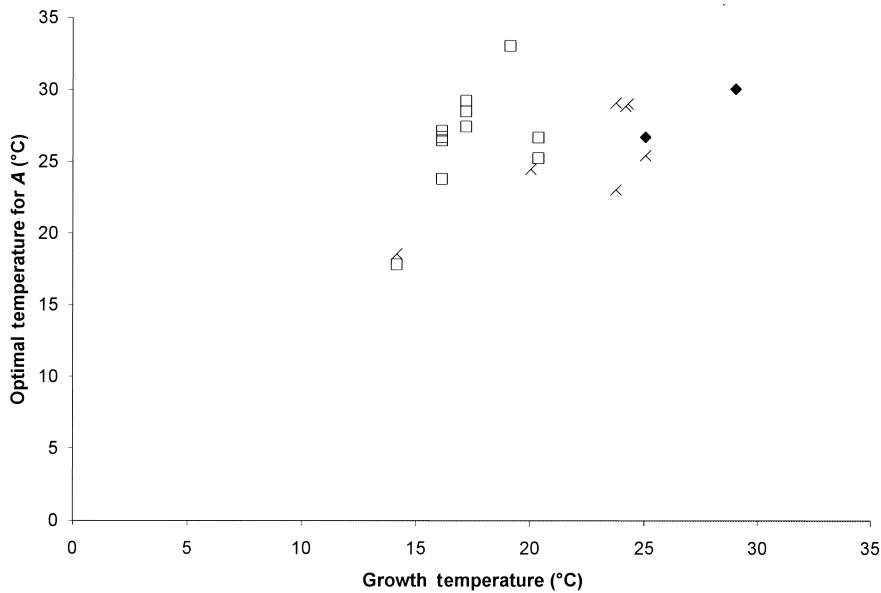


Figure 4. Modelled optimal temperature of light-saturated net photosynthesis plotted against mean temperature in month prior to measurements. Filled symbols: crop species; open symbols: broadleaf species; crosses: coniferous species.

fairly similar responses, falling between those of *A. pseudo-platanus* and *Q. petraea*. The two Finnish trees, *B. pendula* and *P. sylvestris*, had distinctly different responses, with much lower optimal temperatures. Finally, cotton (and to a lesser extent *J. regia*) differed in having a much steeper response curve.

DISCUSSION

The aim of this review was to investigate variability in the temperature responses of the model parameters J_{max} and V_{cmax} , with a view to improving parameter choice when modelling photosynthetic processes. The major factors thought to affect these responses are growth temperature

and genotype or species (Berry & Björkman 1980). It has also been suggested that nutrition (Martindale & Leegood 1997) and light availability (Niinemets *et al.* 1999) may play a role.

We found that the temperature responses of J_{max} and V_{cmax} obtained in gas exchange experiments were quite similar across many of the species included in the review (Tables 2 and 3), a promising finding as it potentially simplifies parameter choice. Parameter values obtained by alternative means (*in vitro*, chlorophyll fluorescence) are included for comparison in Table 4, and generally fall within the range of values reported in Tables 2 and 3. Responses of coniferous and broadleaf trees were broadly similar, with only a slight trend for lower H_a of J_{max} in conifers. However, the responses of the two crop species, par-

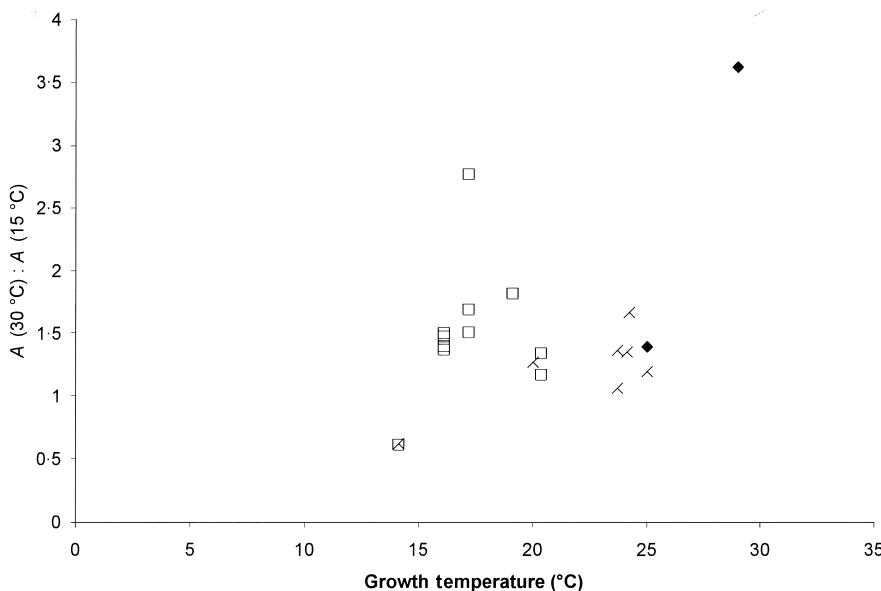


Figure 5. Modelled ratio of light-saturated net photosynthesis at 30 °C to that at 15 °C, plotted against mean temperature in month prior to measurements. Filled symbols: crop species; open symbols: broadleaf species; crosses: coniferous species.

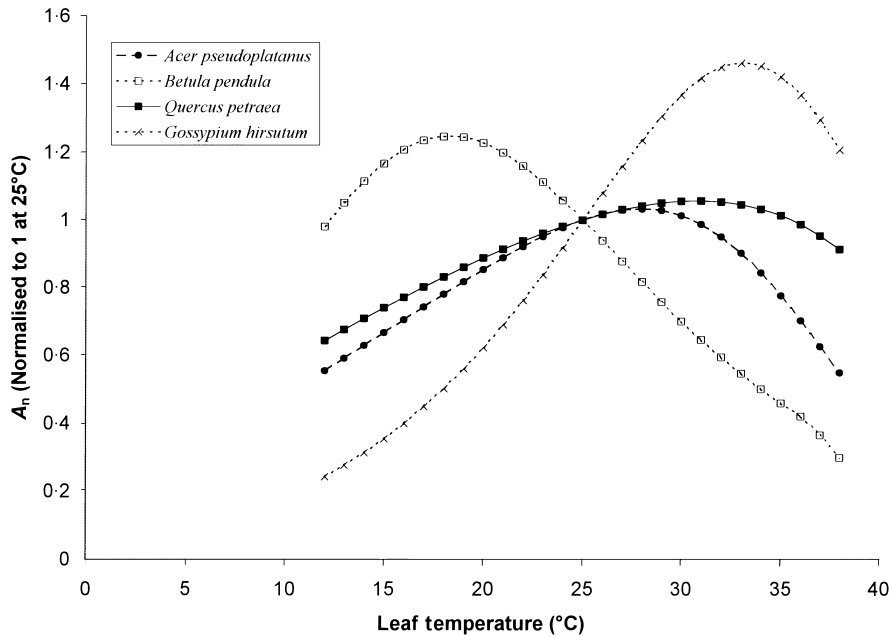


Figure 6. Sample responses of modelled leaf photosynthesis to leaf temperature. Values are normalized to 1 at 25 °C.

ticularly cotton, differed from tree species in several aspects including activation energies of both J_{\max} and V_{\max} and the ratio of $J_{\max} : V_{\max}$ at 25 °C, suggesting that alternative parameter sets are required for modelling these two plant types. This result needs to be clarified by expansion of the database on herbaceous species and crops, however.

It is not possible to draw inferences about acclimation of photosynthesis to growing conditions from such a diverse set of studies, because several alternative explanations are possible for any observed differences, such as differences in experimental protocol or genotypic differences. Nevertheless some interesting comparisons can be made which can serve as a preliminary basis for generalizations about temperature responses in different environments.

For example, we can compare studies on the same species growing in different environmental conditions. Both *Fagus sylvatica* and *Quercus robur* were the subject of two different studies, one with seedlings growing individually in

pots and one with seedlings growing densely in mini-ecosystems. Low foliar nitrogen in the mini-ecosystem studies led to low values of k_{25} for both J_{\max} and V_{\max} . The relative temperature response of V_{\max} was unchanged, but T_{opt} of J_{\max} was lower in the mini-ecosystem experiment. This result parallels that of Niinemets *et al.* (1999) who found that the temperature optimum of J_{\max} was positively correlated with light availability and suggested that the correlation was a result of photosynthetic acclimation to microclimate.

There was generally a poor relationship between parameter values and growth temperature, with the clear exception of the lowest-temperature-grown plants, *B. pendula* and *P. sylvestris*, which had distinctly different temperature responses compared to plants of the same genus grown in temperate climates. The low-temperature-grown plants had low optimal temperatures for both J_{\max} and V_{\max} , and low $J_{\max} : V_{\max}$ ratios. Although not completely comparable, a

Parameter values	Material	Authors		
V_{\max}				
E_a				
58-52	<i>Atriplex glabriscula</i> , purified Rubisco	Badger & Collatz (1977) ¹		
65-33	transgenic <i>Nicotiana tabacum</i>	Bernacchi <i>et al.</i> (2001) ²		
J_{\max}				
H_a	T_{opt}			
65-01	179.2	33.7	<i>Populus tremula</i> , intact leaves	Niinemets <i>et al.</i> (1999) ³
54-97	325.5	40.3	<i>Tilia cordata</i> , intact leaves	Niinemets <i>et al.</i> (1999) ³
37	220	31	barley chloroplasts	Nolan & Smillie (1976) ¹

Table 4. Comparable parameter values obtained by other methods

¹*in vitro*; ²*in vivo* measurements with transgenic low-Rubisco plants; ³chlorophyll fluorescence.

study on alpine grasses growing in low temperature environments (Wohlfahrt *et al.* 1999) does not show such dramatic differences in the temperature optima of J_{\max} and V_{cmax} . Further research is required to clearly establish the effects of growth in a cold climate on the temperature responses of J_{\max} and V_{cmax} . No data were available for tropical species; it would be interesting to see how optimal temperatures for such species compare with those reported here.

Another key requirement for future research highlighted by this study is the need for more information on the temperature dependence of K_c and K_o , the Michaelis–Menten coefficients for Rubisco activity. We have illustrated the fact that values of V_{cmax} derived from gas exchange data depend strongly on the assumed values of K_c and K_o and hence are not readily comparable between studies. In the absence of a clear resolution of the temperature dependence of these parameters, it is important, particularly when modelling, to ensure that parameter sets are consistent (Medlyn *et al.* 1999).

It should be noted that photosynthetic rates are determined not only by biochemical processes, but also by stomatal conductance to CO_2 . In this study we have omitted to consider the effects on photosynthesis of possible acclimation of stomatal conductance to temperature. (Figs 4–6 were constructed assuming a constant $C_i:C_a$ ratio.) In the companion paper (Medlyn, Loustau & Delzon 2002), we showed that changes in stomatal conductance could contribute considerably to photosynthetic temperature acclimation. A similar result was found by Ferrar, Slatyer & Vranjic (1989) for *Eucalyptus* species and Ellsworth (2000) for *Pinus taeda*. Berry & Björkman (1980) suggested stomatal acclimation to temperature was uncommon but also noted that information on this topic was scarce. Even without acclimation, photosynthetic rates at ambient CO_2 concentration at optimum temperature, and the temperature of optimum photosynthesis itself, can be strongly affected by stomatal responses to temperature and water vapour pressure deficits (Kirschbaum & Farquhar 1984). Hence, even with identical photosynthetic parameters, leaves can have different photosynthetic rates under ambient conditions due to different stomatal conductances caused by internal (e.g. water stress) or external (e.g. water vapour pressure deficits) factors. It has also been suggested that changes in the temperature response of cell-wall conductance may be a factor in temperature acclimation (Makino *et al.* 1994). We were unable to evaluate this possibility owing to lack of data.

CONCLUSION

The primary aim of this review of the temperature responses of model parameters J_{\max} and V_{cmax} was to highlight variability in these responses among species and growth environments in order to improve parameter choice when modelling temperature effects on photosynthesis and growth. In general, it was found that parameters for crop

species, temperate trees, and boreal trees, fell into three distinct groups (see Tables 2 and 3), suggesting that modellers should use a set of parameters from the appropriate group. The limited data analysed here also revealed differences in photosynthetic temperature response parameters among growth environments, suggesting that equations should be chosen, where possible, to be appropriate for given radiation and temperature conditions. However, to better model temperature responses, a greater understanding of the functional significance of differences among broad plant types and growth environments is needed, which will require more careful experimental comparisons of within-versus among-species variation in temperature response parameters.

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