

***In vivo* temperature response functions of parameters required to model RuBP-limited photosynthesis**

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ABSTRACT

The leaf model of C₃ photosynthesis of Farquhar, von Caemmerer & Berry (*Planta* 149, 78–90, 1980) provides the basis for scaling carbon exchange from leaf to canopy and Earth-System models, and is widely used to project biosphere responses to global change. This scaling requires using the leaf model over a wider temperature range than that for which the model was originally parameterized. The leaf model assumes that photosynthetic CO₂ uptake within a leaf is either limited by the rate of ribulose-1,5-bisphosphate (RuBP) regeneration or the activity of RuBP carboxylase-oxygenase (Rubisco). Previously we reported a re-parameterization of the temperature responses of Rubisco activity that proved robust when applied to a range of species. Herein this is extended to re-parameterizing the response of RuBP-limited photosynthesis to temperature. RuBP-limited photosynthesis is assumed to depend on the whole chain electron transport rate, which is described as a three-parameter non-rectangular hyperbolic function of photon flux. Herein these three parameters are determined from simultaneous measurement of chlorophyll fluorescence and CO₂ exchange of tobacco leaves, at temperatures from 10 to 40 °C. All varied significantly with temperature and were modified further with variation in growth temperature from 15 to 35 °C. These parameters closely predicted the response of RuBP-limited photosynthesis to temperature measured in both lemon and poplar and showed a significant improvement over predictions based on earlier parameterizations. We provide the necessary equations for use of the model of Farquhar *et al.* (1980) with our newly derived temperature functions for predicting both Rubisco- and RuBP-limited photosynthesis.

Key-words: global change; mathematical model; photosynthesis; Rubisco; temperature response.

INTRODUCTION

The leaf model of photosynthesis presented by Farquhar, von Caemmerer & Berry (1980) assumes that photosynthe-

sis is limited by the slower of two processes: (1) the maximum rate of Rubisco-catalyzed carboxylation; and (2) or the regeneration of RuBP controlled by electron transport rate (RuBP-limited). This model has been used extensively for scaling carbon uptake to canopies (Wang & Jarvis 1990; Amthor 1995; Lloyd & Farquhar 1996; dePury & Farquhar 1997), ecosystems (Field & Avissar 1998), landscapes (Sellers *et al.* 1996, 1997) and the biosphere (Cramer & Field 1999). However, the original model was not parameterized for the range of temperatures to which it is now being applied. Previously, we have shown that re-parameterization of the temperature response of Rubisco-limited photosynthesis using *in vivo* measurements substantially improved the ability of the model to predict leaf CO₂ uptake over a wide range of temperatures (Bernacchi *et al.* 2001). Here we extend this approach to modelling RuBP-limited photosynthesis.

It is commonly accepted that the regeneration of RuBP is highly dependent on whole chain electron transport on the chloroplast thylakoid (Evans 1987; Ögren & Evans 1993; von Caemmerer 2000). The model of Farquhar *et al.* (1980) couples RuBP-regeneration to a mechanistic prediction of electron partitioning between photosynthesis and photorespiration. The rate of whole chain electron transport (J) is predicted as an empirical hyperbolic function of absorbed photon flux (Q) and the efficiency of photon use (Ögren & Evans 1993; von Caemmerer 2000). The non-rectangular hyperbolic response of J to Q is determined by three parameters: J_{\max} is the maximum rate of electron transport that the leaf can support; $\Phi_{\text{PSII},\max}$ is the initial slope of the response and the maximum quantum yield of electron transport through photosystem II; and Θ_{PSII} is the convexity of the transition between the initial slope and the plateau of the hyperbola. The temperature responses of these parameters are critical to model RuBP-limited photosynthesis accurately.

The original parameters used for modelling the response of RuBP-limited photosynthesis to temperature were based on isolated thylakoids (Armond, Schreiber & Björkman 1978). The model therefore assumed that the chemical environment of the assay reflects that of the thylakoid *in vivo*, and that it does not change with light. Yet large changes in pH and Mg²⁺ occur *in vivo* in addition to possible changes in organization of the membrane that may not be mimicked *in vitro*. An alternative approach was to determine J_{\max} *in vivo* from gas-exchange measurements of photosynthesis

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(A) versus intercellular leaf CO₂ concentration (C_i; Harley & Tenhunen 1991; McMurtrie & Wang 1993; Harley & Baldocchi 1995; Ziska 2001; Dreyer *et al.* 2001). This method relies on fitting data measured at higher CO₂ concentrations to the RuBP-limited equation for photosynthesis from the Farquhar *et al.* (1980) model. Estimation of J_{max} from A versus C_i curves is problematic because RuBP-limited photosynthesis is predicted from the very slight changes in A with increase in C_i above the inflection between Rubisco- and RuBP-limited photosynthesis of the response curve.

Previous model parameterizations have not considered that other parameters of the J versus Q relationship may change with temperature, Φ_{PSII,max} and Θ_{PSII}. Yet this may be especially important in predicting light-limited photosynthesis because any change here would have a profound effect on RuBP regeneration under light-limiting conditions. Modelling exercises have assumed a constant Φ_{PSII,max} of 0.85 over a range of temperatures (Farquhar *et al.* 1980; Evans 1989; von Caemmerer 2000). This value is typical of dark-adapted leaves. However, in the field this value is likely to be obtained only at dawn. Additionally, Θ_{PSII} is assumed to remain constant at 0.7 over a range of temperatures (Evans 1989; Ögren & Evans 1993). Fitting the light response curves of CO₂ uptake measured from infrared gas analysis and of whole chain electron transport measured from chlorophyll fluorescence at saturating CO₂ allows direct measurement of the parameters required to model RuBP-limited photosynthesis, without the assumptions needed to estimate these from A versus C_i curves alone. This combined approach provides two independent estimates of J_{max}, one accounting for all electron sinks, and an independent means of separating RuBP-limited photosynthesis from photosynthesis limited by Rubisco or limited by the rate of triose phosphate utilization (TPU) (Harley & Sharkey 1991). Measuring J from fluorescence also provides the opportunity to test if Φ_{PSII,max} and Θ_{PSII} are temperature dependent.

This study uses both gas exchange and chlorophyll fluorescence to determine the temperature responses of J_{max}, Θ_{PSII} and Φ_{PSII,max} over a range of biologically significant temperatures. Because the response of J to instantaneous leaf temperature is known to depend on growth temperature (von Caemmerer 2000), measurements were made on plants grown at 14, 25 and 35 °C.

MODEL THEORY

The symbols used in the model explanation are defined in Appendix 1. The model of leaf photosynthesis (Farquhar *et al.* 1980) states that when CO₂ uptake rate (A) is RuBP limited then:

$$A = (1 - \Gamma^*/C_i) \cdot \frac{J \cdot C_i}{4.5C_i + 10.5\Gamma^*} - R_d \quad (1)$$

where Γ* and R_d are defined as the photosynthetic CO₂ compensation point and mitochondrial respiratory flux, respectively, C_i is intercellular leaf CO₂ concentration and

J is the rate of electron transport. The model assumes that RuBP regeneration is limited by potential whole chain electron transport rate under the given conditions of light and temperature, corrected for partitioning between oxygenation and carboxylation of RuBP. Electron transport (J), in the more recent formulations of the model (von Caemmerer 2000) is expressed as a non-rectangular hyperbola

$$J = \frac{Q_2 + J_{\max} - \sqrt{(Q_2 + J_{\max})^2 - 4 \cdot \Theta_{\text{PSII}} \cdot Q_2 \cdot J_{\max}}}{2 \cdot \Theta_{\text{PSII}}} \quad (2)$$

where Θ_{PSII} represents a curvature factor, J_{max} is the maximum rate of electron transport and Q₂ represents the maximum fraction of incident quanta that could be utilized in electron transport and is given by the equation:

$$Q_2 = Q \times \alpha_l \times \Phi_{\text{PSII,max}} \times \beta \quad (3)$$

where α_l is the leaf absorptance, Φ_{PSII,max} is maximum quantum yield of photosystem II and β is the fraction of absorbed light that reaches photosystem II (Ögren & Evans 1993; von Caemmerer 2000). As currently parameterized, models of RuBP-limited photosynthesis rely on the temperature response of J_{max} (Ögren & Evans 1993; reviewed: Medlyn *et al.* 2002). Values of α_l, Φ_{PSII,max}, β and Θ_{PSII} of Eqns 2 and 3 have been assumed constant over a wide range of leaf temperatures (Farquhar *et al.* 1980; McMurtrie & Wang 1993; Ögren & Evans 1993; Harley & Baldocchi 1995).

MATERIALS AND METHODS

Wild-type tobacco (*Nicotiana tabacum* L. cv. W38) plants were germinated in environmentally controlled greenhouses located at the University of Illinois, Urbana, IL USA. Seeds were sown in 0.9 L plastic containers and were individually transplanted into 1.5 L round pots approximately 2 weeks after emergence. Plants were grown in a soil-less growth medium (Sunshine Mix no. 1; SunGro Horticulture, Inc., Bellevue, WA, USA) and were watered daily. Nutrient additions were applied weekly in the form of 300 μL L⁻¹ of NPK 15: 5: 15 (Peters Excel; The Scotts Co., Marysville, OH, USA) to pot saturation. After transplanting, seedlings were placed into environmentally controlled growth chambers (Conviron E15; Controlled Environments, Inc., Pembina, ND, USA). Growth-chamber air temperatures were set to 14/10, 25/20 and 35/28 °C (day/night). In all chambers, relative humidity was held constant at 70% and Q at 500 μmol m⁻² s⁻¹ during the 16 h photoperiod. Twice weekly, the treatments and plants were switched between the chambers to minimize any confounding effects that undetected differences between the individual chambers could have on the treatments.

An open gas-exchange system with a 2-cm² clamp-on leaf cuvette was used to simultaneously measure gas exchange and chlorophyll fluorescence (LI-6400 and LI-6400-40; Li-Cor, Inc., Lincoln, NE, USA). Measurements were taken at leaf temperatures ranging from 10 to 40 °C in increments of 5 °C, and additional measurements were made at 37.5 °C. The chamber was modified by replacing

the Peltier external heat sink with a metal block containing water channels, which were connected to a heating/cooling circulating water bath (Bernacchi *et al.* 2001). The youngest fully expanded leaves, attached to the plant, were sealed in the leaf chamber for a minimum of 20 min in the dark. After this dark-adaptation, the maximum dark-adapted quantum yield of photosystem II ($\Phi_{\text{PSII,max}}$) was determined from the measured induction of chlorophyll fluorescence. Leaves were then light adapted for 20 min at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ Q . Gas exchange measurements were coupled with fluorescence to simultaneously measure the responses of J and A to Q . Measurements were performed at a saturating CO_2 concentration of $2000 \mu\text{mol mol}^{-1}$ in the air surrounding the leaf to ensure that photosynthesis was RuBP-regeneration limited. Saturation was confirmed by showing that J remained constant with change in CO_2 concentration around $2000 \mu\text{mol mol}^{-1}$. Gas exchange parameters A were calculated using the equations of von Caemmerer & Farquhar (1981). Photochemical efficiency of photosynthesis (Θ_{PSII}) was determined by measuring both steady-state fluorescence (F_s) and maximum fluorescence during a light saturating pulse (F_m') on light-adapted leaves following the procedures of Genty, Briantais & Baker (1989):

$$\Phi_{\text{PSII}} = 1 - F_s/F_m' \quad (4)$$

The rate of whole chain electron transport (J) for the leaf was then calculated as:

$$J = \Phi_{\text{PSII}} \cdot Q \cdot \alpha_l \cdot \beta \quad (5)$$

where α_l is the leaf absorptance and β is the fraction of absorbed quanta that reaches photosystem II (assumed to be 0.5 for C_3 plants; after Ogren & Evans 1993; von Caemmerer 2000). Leaf absorptance (α_l) was calculated as:

$$\alpha_l = \alpha_b B + \alpha_r(1 - B) \quad (6)$$

Terms α_b and α_r , which represent the measured leaf absorptance at the blue and red light wavelengths emitted from the gas exchange system light source (LI-6400-40), were determined for each leaf with an integrating sphere attached to a spectroradiometer (LI-1800; Li-Cor, Inc.). B is the proportion of light in the blue wavelengths. Because the ratio of red to blue light varied based on levels of Q , values for α_l were calculated for each Q .

After 20 min of light adaptation at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ Q , both A versus Q and J versus Q curves were constructed by starting at the highest levels of Q ($2000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and decreasing step-wise to $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. At lower leaf temperatures, the maximum Q was $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$; this was found necessary to prevent photo-inhibition (Long, Humphries & Falkowski 1994; Werner, Ryel & Beyschlag 2001) or/and TPU-limitation (Harley & Sharkey 1991) from occurring. For all measurements, light was provided by the red and blue LEDs integrated into the leaf chamber fluorometer (LI-6400-40). The A versus Q curves were fitted using Eqn (2) modified to represent photosynthesis rather than electron transport parameters as:

$$A = \frac{Q\Phi_a + A_{\text{max}} - \sqrt{(Q\Phi_a + A_{\text{max}})^2 - 4\Theta Q\Phi_a A_{\text{max}}}}{2\Theta} \quad (7)$$

where Φ_a is the maximum quantum yield of CO_2 assimilation, A_{max} is light and CO_2 saturated photosynthesis, and Θ is a convexity term (Long & Hällgren 1993). Because A_{max} represents light- and CO_2 -saturated photosynthesis, it was used to solve for $J_{\text{max,c}}$ by rearranging Eqn (1) to:

$$J_{\text{max,c}} = \frac{(A_{\text{max}} + R_d)(4.5C_i + 10.5\Gamma^*)}{(C_i - \Gamma^*)} \quad (8)$$

Both Γ^* and R_d are highly temperature dependent; the functions describing these temperature dependencies were taken from Bernacchi *et al.* (2001). Curves of J versus Q were fitted to Eqns 2 and 3. We term the initial linear portion of the J versus Q curve taken on a light-adapted leaf $\Phi_{\text{PSII,max,l}}$ to distinguish it from the maximum efficiency of PSII of a dark-adapted leaf ($\Phi_{\text{PSII,max}}$).

Temperature functions

The generic temperature response functions for the various parameters were fitted to the equation:

$$\text{Parameter} = \text{Parameter}_{25} \times \exp^{(c - \Delta H_a / (R(T_1 + 273)))} \quad (9)$$

to solve for the scaling constant (c) and the energy of activation (ΔH_a ; Sharpe & DeMichele 1977; Harley & Tenhunen 1991; Leuning 1997). Parameter_{25} is the absolute value of the parameter at 25°C . Use of this equation assumes that the activity will continue to increase exponentially with temperature (Sharpe & DeMichele 1977; Harley & Tenhunen 1991; Leuning 1997; Medlyn *et al.* 2002). If any parameter decreased at higher temperature, a phenomena consistent with de-activation, Eqn 9 was modified to include terms for entropy (ΔS) and energy of de-activation (ΔH_d) as described previously (Harley & Tenhunen 1991):

$$\text{Parameter} = \text{Parameter}_{25} \cdot \frac{\exp^{(c - \Delta H_a / (R(T_1 + 273)))}}{1 + \exp^{[(\Delta S \cdot (T_1 + 273) - \Delta H_d) / R(T_1 + 273)]}} \quad (10)$$

All measured temperature responses were fitted to Eqn 9, or to Eqn 10 where an optimum was observed at or below 40°C , by maximum-likelihood regression (Regression Analysis Function, SigmaPlot 6.1; SPSS, Inc., Chicago, IL, USA). In addition $J_{\text{max,c}}$, $J_{\text{max,f}}$ and Θ_{PSII} were also fitted to a Gaussian 3-D function to describe modification of the response to T_1 by T_g (SigmaPlot 6.1; SPSS, Inc.).

Model validation

A test of the temperature functions derived in this study from tobacco was made against the measured temperature response of photosynthesis of lemon (*Citrus limon* L.) and measured diurnal rates of photosynthesis for poplar [*Populus × euramericana* Dode (Guinier)]. Three lemon trees were grown in a controlled-environment greenhouse with 16 h photoperiods and daily minimum Q of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Nutrients were applied weekly, as for the tobacco, and the trees were watered as needed.

Photosynthesis was measured using an open gas-exchange system as outlined above for tobacco using a C_i sufficient to ensure RuBP-limited photosynthesis. Response curves of photosynthesis to CO_2 were determined from one leaf of each of three lemon trees at 10–40 °C in 5 °C increments. Rates of photosynthesis from the RuBP-limited portion of these response curves were used for the validation. The response curves measured at 25 °C provided the absolute values of J_{max} from which the modelled values were generated. These were then compared with the values measured between 10 and 40 °C.

The diurnal response of poplar [*Populus × euramericana* Dode (Guinier)] leaf photosynthesis was measured during July 2000 at the Poplar Free Air gas Concentration Enrichment (POPFACE) research facility (Miglietta *et al.* 2001). Measurements were made using a portable gas exchange system (LI-COR 6400; Li-Cor, Inc.) with a clear chamber head to allow for natural sunlight to illuminate the leaf. Beginning at predawn and finishing after dusk, photosynthesis of two leaves per plot were measured in the elevated CO_2 (550 $\mu\text{mol mol}^{-1}$) plots at approximately 1 h intervals. Measurements were made at this CO_2 concentration because parallel measurements of A versus C_i responses indicated that leaves would be RuBP limited for most of the day in this treatment. Measurements were confined to the youngest fully expanded leaf and were measured in a horizontal position to minimize variation between leaves at any point in time (Garcia *et al.* 1998). Upon placing the leaf in the cuvette, a stabilization period of at least 40 s was used prior to measurements. This ensured steady-state photosynthesis measurements while avoiding significant increases in leaf temperature. Plots of A versus C_i were measured within 2 d of the diurnal measurements and provided values of $V_{c,max}$ and J_{max} at 25 °C to implement into the leaf model of photosynthesis. Modelled diurnal rates of photosynthesis

were created using the temperature dependencies provided by Farquhar *et al.* (1980) and using the dependencies developed in this study and from Bernacchi *et al.* (2001).

Statistical methods

Three separate groups of comparisons were made: (1) the effect of T_g on the response of J_{max} to T_i (absolute and normalized to unity at 25 °C) fitted to either Eqn (9) or (10); (2) the regression of $J_{max,c}$ against $J_{max,f}$; and (3) the effect of T_g on the responses of $\Phi_{PSII,max}$, $\Phi_{PSII,max,l}$, and Θ_{PSII} to T_i . Differences in temperature responses were tested by the comparison of regressions technique of Mead & Curnow (1983). Using this statistical method, the relationships between the three growth temperatures were first fitted using non-linear regression (NLIN Procedure, SAS 8.1; The SAS Institute, Inc., Cary, NC, USA). Next, the goodness-of-fit for a separate curve representing each growth temperature was compared with the goodness-of-fit for one curve representing the three growth temperatures combined. The type three sums of squares (i.e. error variances around each model) and associated degrees of freedom for combined versus separate fits were used to compute F -ratios associated with the residuals of these fits (Mead & Curnow 1983; Potvin, Lechowicz, & Tardif 1990).

RESULTS

Temperature response of J_{max}

The value of $J_{max,c}$ increased linearly and 1 : 1 with $J_{max,f}$ for leaves grown at 25 and 35 °C, but increased only at 0.9 : 1 for leaves grown at 14 °C ($F_{2,94} = 7.31$, $P < 0.01$; Fig. 1). Both $J_{max,f}$ and $J_{max,c}$ increased continuously to 40 °C with increase

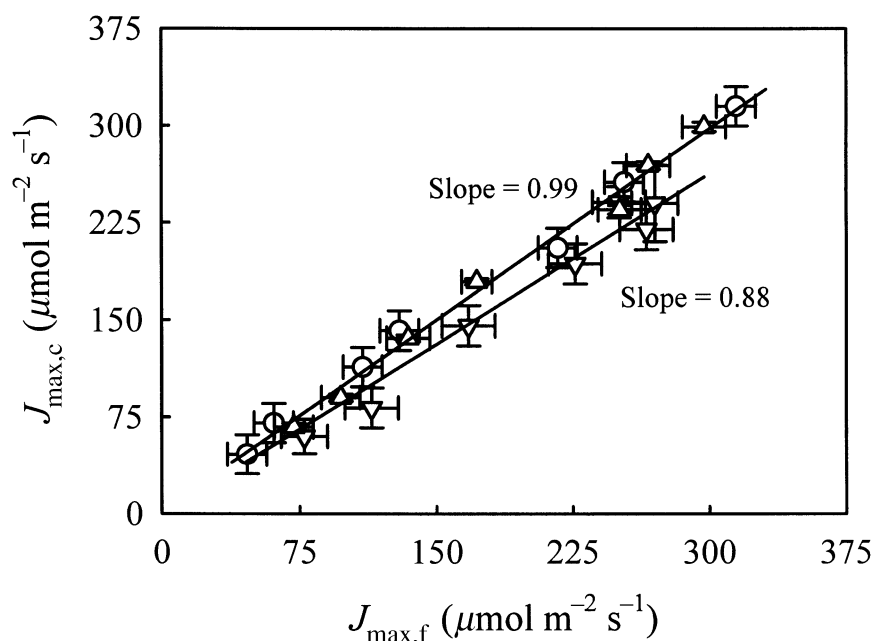


Figure 1. The linear relationship between the maximum rate of electron transport (J_{max}) estimated from gas exchange measurements ($J_{max,c}$) and that estimated from fluorescence measurements ($J_{max,f}$) for plants grown in 14 °C (∇), 25 °C (\circ) and 35 °C (Δ). Points are the mean of at least three replicate J_i/Q and A/Q responses from T_i 10–40 °C for each T_g . Vertical and horizontal bars indicate ± 1 SE of the mean. Lines are fitted to the response of $J_{max,c}$ to $J_{max,f}$.

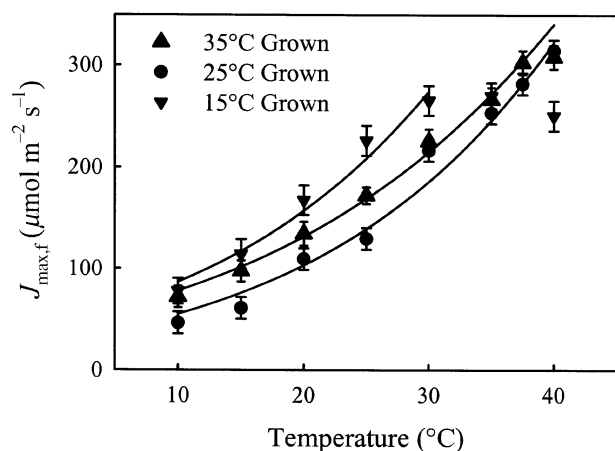


Figure 2. The response of maximum electron transport through PSII ($J_{\max,f}$) to leaf temperature (T_l) for plants grown in 14 °C (▼), 25 °C (●) and 35 °C (▲). Regression lines were fit using Eqn 9. Error bars indicate ± 1 SE of the mean.

in T_l , except for the plants grown at 14 °C, where a plateau was reached at 30 °C (Fig. 2). The response to T_l was significantly altered by T_g ($F_{4,86} = 8.13$, $P < 0.001$). The temperature responses of $J_{\max,f}$ within each of the three growth temperatures were normalized to unity at 25 °C to determine relative changes in the pattern of response. The response of J_{\max} up to a T_l of 30 °C was similar for both the 14 and 25 °C-grown plants (Fig. 3; $F_{2,36} = 0.12$, $P > 0.9$; Table 1). The normalized response of $J_{\max,f}$ to T_g and T_l were fitted to a Gaussian 3-D function given in Eqn 11 ($F_{4,87} = 231.64$, $P < 0.001$):

$$J_{\max,f} = 1.91 \cdot \exp^{(0.5 \cdot (((T_g - 26.69)/15.75)^2 + ((T_l - 49.07)/21.29)^2))} \quad (11)$$

The normalized temperature response of $J_{\max,c}$ for each T_g was similarly fit to a Gaussian 3-D function ($F_{4,87} = 156.51$, $P < 0.001$):

$$J_{\max,c} = 1.92 \cdot \exp^{(-0.5 \cdot (((T_g - 26.42)/17.97)^2 + ((T_l - 47.04)/19.38)^2))} \quad (12)$$

$\Phi_{\text{PSII,max}}$, $\Phi_{\text{PSII,max,l}}$ and Θ_{PSII}

There were only very slight (< 5%) differences in $\Phi_{\text{PSII,max}}$ with T_g and T_l (Fig. 4a). A slight decrease in $\Phi_{\text{PSII,max}}$ with T_l occurred at 40 °C (Fig. 4a). By contrast, $\Phi_{\text{PSII,max,l}}$ increased with temperature until a T_l of about 25 °C at which point the response of $\Phi_{\text{PSII,max,l}}$ to T_l reaches a plateau (Fig. 4b; Table 2). This response did not vary with T_g ($F_{2,70} = 1.17$, $P > 0.3$).

Convexity (Θ_{PSII}) was found to be highly dependent on both T_l ($F_{6,66} = 8.36$, $P < 0.001$) and T_g ($F_{12,66} = 3.94$, $P < 0.001$; Fig. 4c; Table 2). The response of Θ_{PSII} to T_l and T_g is described by the Gaussian 3-D function of Eqn 13 ($F_{4,82} = 14.18$, $P < 0.001$):

$$\Theta_{\text{PSII}} = 0.85 \cdot \exp^{(-0.5 \cdot (((T_g - 25.8)/14.84)^2 + ((T_l - 29.2)/17.99)^2))} \quad (13)$$

Model validation

RuBP-limited photosynthetic CO_2 uptake (A) was measured at 10–40 °C on leaves of three lemon trees. In addition, absolute values of the parameters describing the response of J to Q (Eqn 2) were determined at 25 °C. These were then used with the above functions determined for tobacco, and previously published temperature functions, to predict RuBP-limited photosynthesis at 10–40 °C. Devi-

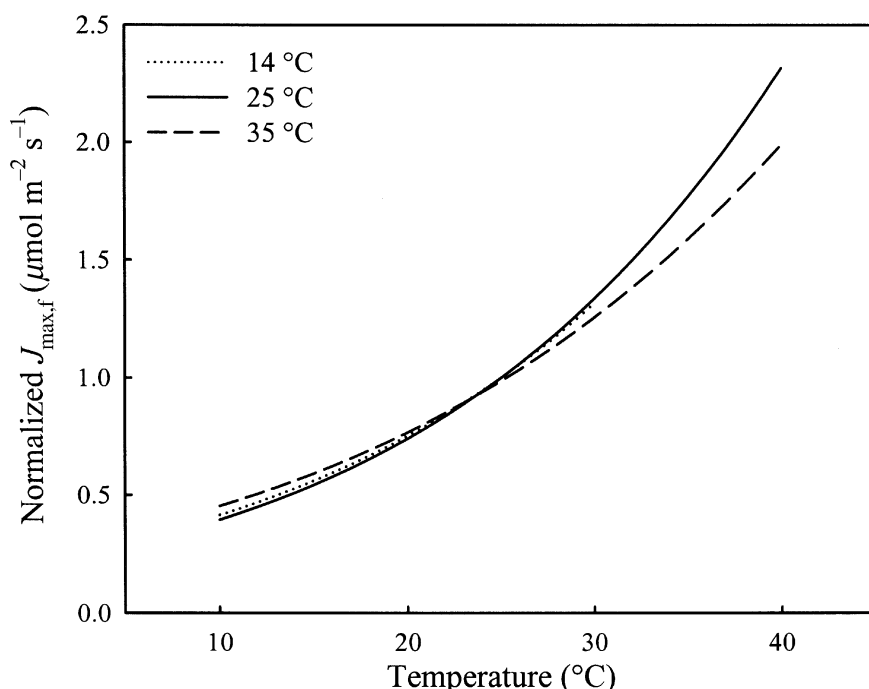


Figure 3. The response of $J_{\max,f}$ to T_l for plants grown in 14, 25 and 35 °C normalized to unity at 25 °C.

Table 1. Values describing the temperature response of J_{\max} to leaf temperature (T_l) determined from gas exchange ($J_{\max,c}$) and chlorophyll fluorescence ($J_{\max,f}$) for growth temperatures (T_g) of 14, 25 and 35 °C

T_g	$J_{\max,c}$				$J_{\max,f}$			
	c	ΔH_a	ΔH_d	ΔS	c	ΔH_a	ΔH_d	ΔS
14 °C	23.2	57.5	439.8	1.4	22.2	54.9	437.7	1.4
25 °C	17.7	43.9	na	na	17.57	43.5	na	na
35 °C	13.9	34.4	na	na	13.22	32.8	na	na

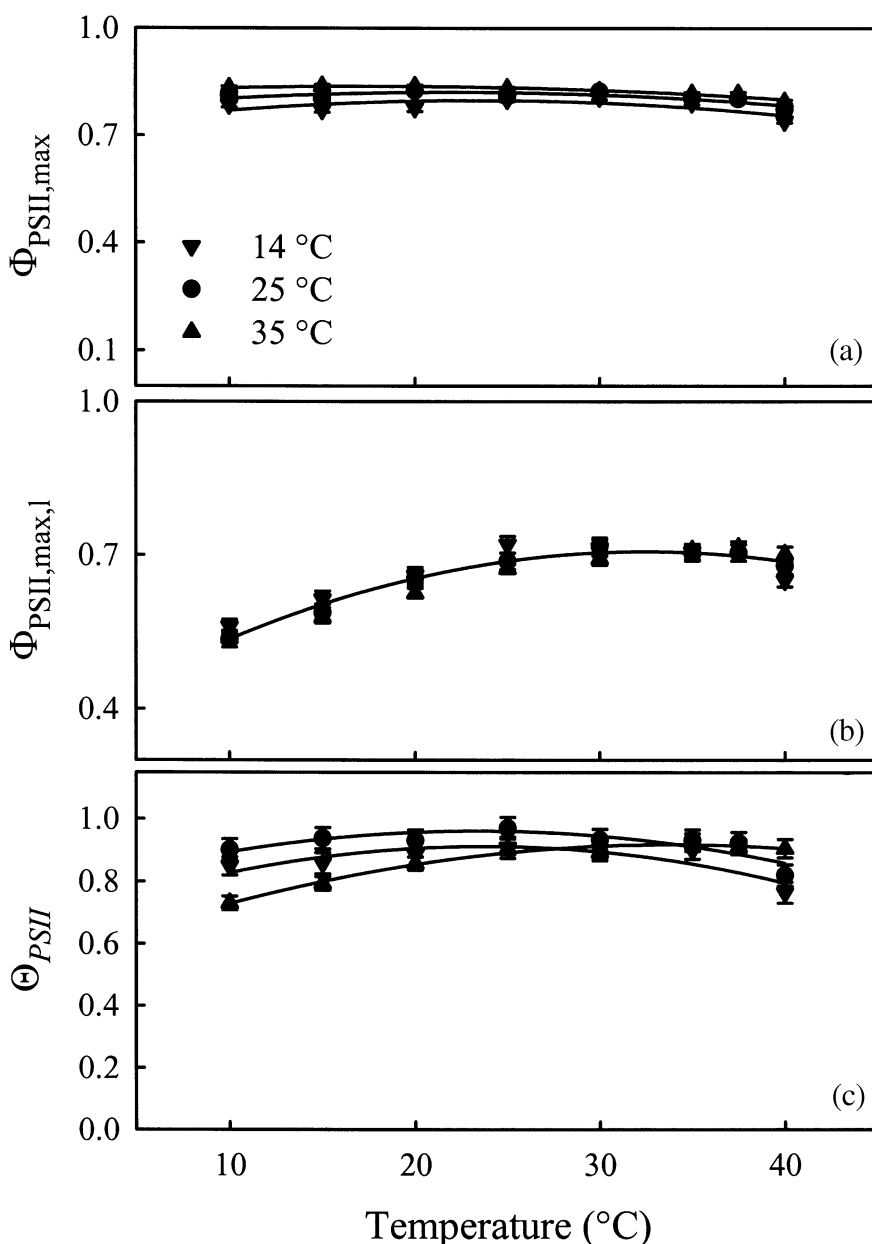
Temperature responses of J_{\max} are fitted to Eqn 9 when only a scaling constant (c) and activation term (ΔH_a) are needed and to Eqn 10 when de-activation (ΔH_d) and entropy (ΔS) terms are also needed. na, Not applicable because J_{\max} increased continuously from 10 to 40 °C.

Table 2. Responses of $\Phi_{\text{PSII,max,l}}$ and Θ_{PSII} to leaf temperature (T_l) for growth temperatures (T_g) of 14, 25 and 35 °C

T_g	$\Phi_{\text{PSII,max,l}}$	Θ_{PSII}
14 °C	$0.352 + 0.021 T_l - 3.4 \times 10^{-4} T_l^2$	$0.66 + 0.021 T_l - 4.5 \times 10^{-4} T_l^2$
25 °C	$0.352 + 0.022 T_l - 3.4 \times 10^{-4} T_l^2$	$0.76 + 0.018 T_l - 3.7 \times 10^{-4} T_l^2$
35 °C	$0.352 + 0.022 T_l - 3.4 \times 10^{-4} T_l^2$	$0.54 + 0.023 T_l - 3.3 \times 10^{-4} T_l^2$

ations of the predicted values from the measured values, standardized on the rate at 25 °C are shown in Fig. 5.

Comparisons of the measured rates of photosynthesis and rates modelled using the Farquhar *et al.* (1980) model of photosynthesis with the original parameters shows that the model significantly underestimated photosynthesis at

**Figure 4.** The responses to leaf temperature (T_l) of: (a) maximum quantum efficiency of photosystem II ($\Phi_{\text{PSII,max}}$) from dark-adapted leaves; (b) apparent $\Phi_{\text{PSII,max}}$ of light-adapted leaves ($\Phi_{\text{PSII,max,l}}$); and (c) Θ_{PSII} fitted from curves of J versus Q . Each point represents the mean of at least three plants for each T_g and error bars represent ± 1 SE of the mean.

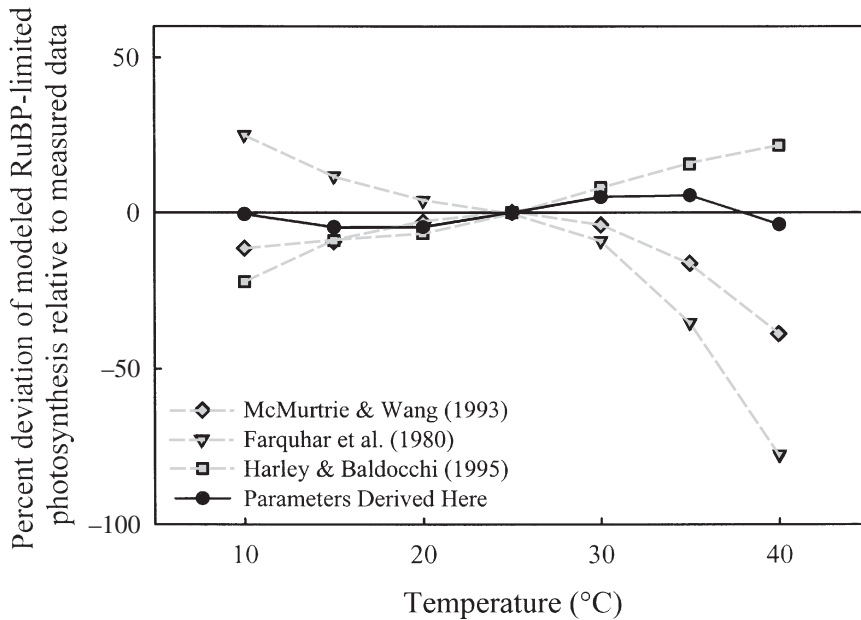


Figure 5. Percentage deviation of modelled leaf CO_2 uptake (A) versus A measured under RuBP-limited conditions for lemon. Modelled values represent three previously published model parameterizations and the parameterizations derived in this study. Both the modelled responses and the experimental data are normalized to their values at 25 °C. Mean rates of photosynthesis were $11.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 25 °C.

most diurnal time points (Fig. 6). This is because leaf temperature from 0800 h. until darkness exceeds 25 °C where the parameters of the original Farquhar *et al.* (1980) model for RuBP-limited photosynthesis appear to underestimate A (Fig. 5). Using the temperature functions derived in this study, with parameters developed in Bernacchi *et al.* (2001), the relationship between the measured and modelled rates of photosynthesis are improved, with few modelled values deviating from the standard error bars of the measured values (Fig. 6).

Appendix 2 combines the functions, determined here and in Bernacchi *et al.* (2002). This constitutes a full set of equations to predict $V_{c,\text{max}}$, J_{max} , Θ and Φ at temperatures from 10 to 40 °C for estimating leaf photosynthesis with the model of Farquhar *et al.* (1980) as modified by von Caemmerer (2000).

DISCUSSION

The objective of the study was to determine the *in vivo* temperature dependencies of the parameters necessary to model RuBP-limited photosynthesis and to determine whether these parameters acclimate to altered growth temperature. By combining gas-exchange and fluorescence approaches, temperature dependencies determined in tobacco predicted the response of RuBP-limited photosynthesis in lemon to within $\pm 5\%$, compared to deviations of up to 20–70% with three previously published temperature functions (Fig. 5). In addition, we have shown that parameters determining RuBP-limited photosynthesis under light-limiting conditions are not constant, in contrast to assumptions made in predicting the response of light-limited photosynthesis to temperature with the model of

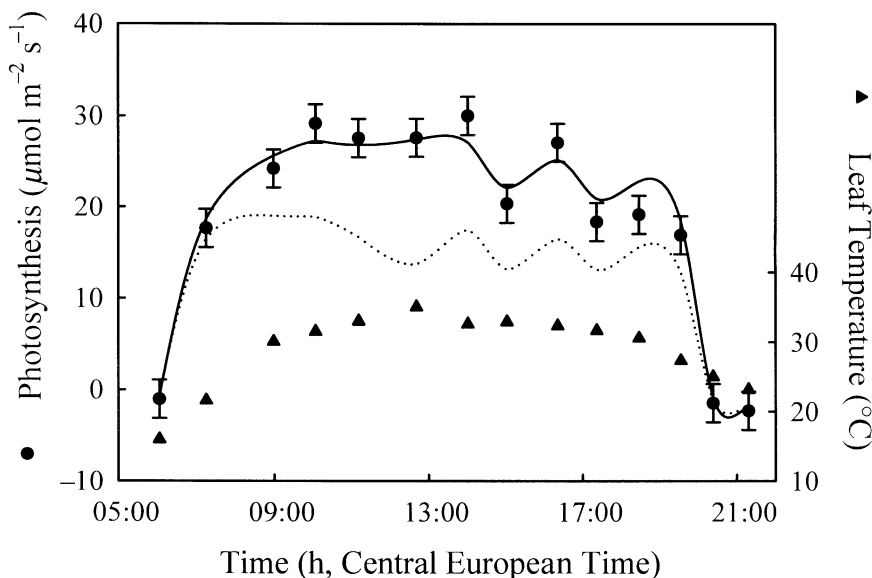


Figure 6. Modelled and measured rates of photosynthesis over a diurnal time course for *Populus x euramericana* grown and measured at $550 \mu\text{mol mol}^{-1} \text{CO}_2$ at the Poplar Free Air gas Concentration Enrichment (POPFACE) research facility. Measured values are represented by closed symbols (± 1 SE). Modelled values were calculated using the leaf model of photosynthesis as originally parameterized (Farquhar *et al.* 1980; dotted line) and using the temperature functions developed in this study and in Bernacchi *et al.* (2001; solid lines). Leaf temperatures for this day varied from 20 to 35 °C (triangle symbols).

Farquhar *et al.* (1980). The temperature in which the plants are grown further modifies the responses.

Temperature response of J_{\max}

Despite the different responses of J_{\max} to increasing leaf temperature in the three growth treatments, all showed maximum values of approximately $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ when measured at 40°C (Fig. 2). The 14°C -grown plants consistently demonstrated higher values of J_{\max} up to 30°C than the plants grown at 25 and 35°C . Medlyn *et al.* (2002) showed apparent species differences in comparing the responses of J_{\max} to temperature from different studies. Herein we show variation in this response for a single genotype grown at different temperatures.

Alternative electron sinks

Using the measurements of A_{\max} to estimate the temperature response of J_{\max} ($J_{\max,c}$) assumes that all electrons are used in photosynthesis and photorespiration. If a significant portion of the electrons are partitioned to alternative sinks, that is processes other than photosynthesis or photorespiration, then $J_{\max,c}$ will be less than J_{\max} estimated using chlorophyll fluorescence ($J_{\max,f}$). This difference represents the flux to alternative sinks (Loreto *et al.* 1994; Laisk & Loreto 1996). Because the measurements made in this study were at saturating CO_2 , mesophyll conductance or any other diffusive process should not, by definition, impose any limitation on photosynthesis. Alternative sinks account for at most 1% of electron transport at growth temperatures of 25 and 35°C but account for a significant (10%) portion of electron transport in plants grown at 14°C (Fig. 1). Tobacco, like maize, originated from the subtropics and may be poorly adapted to low growth temperatures. Maize grown at suboptimal temperatures shows highly significant partitioning to alternative sinks, which are absent at optimal growth temperatures (Fryer *et al.* 1998). Alternatively, it is possible that growth at lower temperatures alters the proportion of absorbed quanta going to PSII (β). For example, if $J_{\max,c}$ were recalculated using a β of 0.44 (Eqn 8), suggesting that a lower proportion of quanta are reaching PSII than PSI, then the relationship between $J_{\max,c}$ and $J_{\max,f}$ for 14°C -grown plants, shown in Fig. 1, will approach unity.

If alternative electron sinks are present in the 14°C -grown plants, it is probably attributed to the Mehler reaction, which occurs when a superoxide forms via the reduction of O_2 , particularly in response to high light fluxes (Furbank & Badger 1983; Miyake *et al.* 1998; Asada 2000; Badger *et al.* 2000; Ort & Baker 2002). If the Mehler reactions or other alternative sinks are present in the 25 and 35°C -grown plants, it is not sufficiently large to be observed. Plants grown in 25 or 35°C measured in colder temperatures might theoretically increase electron partitioning to alternative sinks due to lower photosynthesis and photorespiration rates (Badger *et al.* 2000), however, no evidence of this has been observed in this or in some previous studies (Fig. 1; Ruuska *et al.* 2000; Badger *et al.* 2000).

$\Phi_{\text{PSII,max}}$ and $\Phi_{\text{PSII,max,l}}$

The constancy of $\Phi_{\text{PSII,max}}$ with leaf temperature has been reported for other species (Epron 1997; Dreyer *et al.* 2001). At leaf temperatures of 40°C , the small, yet statistically significant, drop in $\Phi_{\text{PSII,max}}$ is probably in response to increased heat dissipation associated with photosystem II (Fig. 4a; Demmig *et al.* 1998). The effect of growth temperature on $\Phi_{\text{PSII,max}}$ shows that photochemistry for leaves grown at lower temperatures is less efficient; however, at most there is only a 1–2% decrease in $\Phi_{\text{PSII,max}}$ with a 10°C change in growth temperature (Fig. 4a). Changes that occur in thylakoid membrane composition with low growth temperatures may be responsible for the small observed decrease in $\Phi_{\text{PSII,max}}$ (Moon *et al.* 1995). Despite dark-adapted $\Phi_{\text{PSII,max}}$ remaining constant with leaf temperature, light adapted $\Phi_{\text{PSII,max,l}}$ does change significantly with T_l but is unaffected by T_g . This has important implications for modelling light-limited photosynthesis in field conditions.

Implications for modelling RuBP-limited photosynthesis

Because the temperature response of J_{\max} is shown to vary depending on growth conditions (Figs 2 & 3), it is critical that these changes be reflected in the leaf model of photosynthesis. Despite the similarities in the initial portion of the normalized temperature response of J_{\max} to T_l for all T_g , it is clear that the lower values at T_l above 30°C in the plants grown at 35°C , if ignored, would cause overestimation. Despite the possible presence of alternative electron sinks in the leaves grown at 14°C , the relative temperature responses of $J_{\max,f}$ and $J_{\max,c}$ show similar relative changes with temperature. This suggests that either temperature dependency would be appropriate for modelling RuBP-limited photosynthesis. The 25 and 35°C -grown plants both demonstrate an absence of alternative electrons sinks again suggesting that either $J_{\max,f}$ or $J_{\max,c}$ could be successfully applied to the leaf model. Therefore, adjusting the temperature response of $J_{\max,c}$ to the mean growth temperature, through the implementation of the Gaussian function (Table 1) will improve estimates with leaf photosynthesis models.

A common limitation in applying the Farquhar *et al.* (1980) model to vegetation in the field is that mesophyll liquid-phase diffusive conductance is rarely known (Bernacchi *et al.* 2001, 2002). Therefore modelled values will be affected by the assumption that $C_c = C_i$. However, when photosynthesis is RuBP-limited it is typically either approaching CO_2 saturation, when an error in C_c would have minimum impact, or light limited, where C_i and C_c will differ little at the low fluxes of CO_2 .

Previously, a constant value of $\Phi_{\text{PSII,max}}$ (0.85) has been integrated into the leaf models of RuBP-limited photosynthesis (von Caemmerer 2000). The results presented here confirm that T_g and T_l have little effect on $\Phi_{\text{PSII,max}}$ and yield a value close to the 0.85 commonly assumed. We contend, however, that $\Phi_{\text{PSII,max,l}}$ obtained from the light-adapted

leaves, which is consistently lower than $\Phi_{\text{PSII,max}}$ is the relevant measure that should be used in modelling RuBP-regeneration. In a natural environment, $\Phi_{\text{PSII,max}}$ may only be relevant when leaves begin photosynthesizing at dawn. Decreases of Q in nature, by definition only occur when leaves are light adapted. Therefore, values of $\Phi_{\text{PSII,max,l}}$ are probably more appropriate for modelling leaf and canopy photosynthesis in the natural environment. This distinction between $\Phi_{\text{PSII,max}}$ and $\Phi_{\text{PSII,max,l}}$ would have most significance at low T_l where the differences are most marked. The increase in $\Phi_{\text{PSII,max,l}}$ from about 0.55 at 10 °C to 0.7 at 30 °C would have a large impact on predicted J for low light environments in cold temperatures with far less effect in high temperatures. This is consistent with frequent observations that recovery of Φ_{PSII} is far more rapid in warm versus cold conditions (Long *et al.* 1994).

Previous studies have suggested that Θ depends on a range of factors, including chlorophyll content (Leverenz 1987), light acclimation (Terashima 1989), photo-inhibition (Ögren & Sjöström 1990), stomatal conductance (Olsson & Leverenz 1994), CO_2 concentration (Leverenz 1988; Ögren & Evans 1993) and leaf temperature (Leverenz 1988). These previous studies rely on estimates from A versus Q curves (Ögren & Evans 1993), which may be affected by the balance between photorespiration and photosynthesis, and stomatal patchiness. The RuBP-limited model, however, relies on the convexity of the response of electron transport to Q (Θ_{PSII}). Here, we show a dependency of Θ_{PSII} on T_g and T_l . This contrasts with the assumption of previous parameterizations that Θ is constant with temperature (McMurtrie & Wang 1993; Harley & Baldocchi 1995).

Rubisco-limited photosynthesis is governed largely by the properties of a single enzyme, which is highly conserved across C_3 higher plants (Bainbridge *et al.* 1995; Delgado *et al.* 1995). Therefore functions predicting variation in Rubisco-limited photosynthesis would be expected to be robust across species and growth conditions (Bernacchi *et al.* 2001); nevertheless clear thermal adaptation is seen when responses of Rubisco-limited photosynthesis for different species are compared (Medlyn *et al.* 2002). By contrast, RuBP-limited photosynthesis may be determined by a range of processes, which are likely to acclimate to growth conditions (von Caemmerer 2000), including temperature prehistory. We show that *in vivo* parameterization from the annual crop tobacco can nevertheless closely predict the observed temperature response of RuBP-limited photosynthesis in both lemon (Fig. 5) and poplar (Fig. 6). However, we also show that growth of tobacco at a suboptimal temperature modifies the response of RuBP-limited photosynthesis to leaf temperature. This suggests that in contrast to Rubisco-limited photosynthesis, acclimation will introduce errors in using the Farquhar *et al.* (1980) model to scale RuBP-limited photosynthesis to the varying leaf temperatures of the natural environment. This error cannot be defined without studies of a wide range of species and growth temperatures. In the absence of such information, we provide functions, based on tobacco, that account for acclimation to growth temperature. For the first-time in this

context, we also provide equations to predict how light-limited electron transport rates estimated within the model will vary with leaf and growth temperature.

ACKNOWLEDGMENTS

The authors thank Victoria Wittig, Elizabeth Ainsworth, Shawna Naidu, Archie Portis and Donald Ort for comments made on draft versions of this manuscript. C.J.B. was supported by an assistantship from National Science Foundation award DBI 96-02240 'Integrative Photosynthesis Research Training Program'.

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Received 14 January 2003; received in revised form 3 March 2003; accepted for publication 10 March 2003

APPENDIX

Symbols

A	Net rate of CO ₂ uptake per unit leaf area ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
A_{max}	Light and CO ₂ saturated photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
B	Proportion of light at 464 nm (dimensionless, 0–1)
c	Scaling constant (dimensionless)
C_i	Intercellular CO ₂ concentration ($\mu\text{mol mol}^{-1}$)
F_m'	Maximum fluorescence (relative units)
F_s	Steady-state fluorescence (relative units)
J	Rate of electron transport ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
J_{max}	Maximum rate of electron transport ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
$J_{\text{max},c}$	J_{max} estimated from carbon assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
$J_{\text{max},T}$	J_{max} corrected to temperature T
$J_{\text{max},f}$	J_{max} estimated from chlorophyll fluorescence ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
K_c	Michaelis constant for CO ₂ ($\mu\text{mol mol}^{-1}$)
K_o	Michaelis constant for O ₂ (mmol mol^{-1})
Q	Photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
R	Molar gas constant ($\text{kJ K}^{-1} \text{mol}^{-1}$)
R_d	Mitochondrial respiration rate in the light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
$R_{d,T}$	R_d corrected to temperature T
T_g	Growth temperature ($^{\circ}\text{C}$ or K)
T_l	Leaf temperature ($^{\circ}\text{C}$ or K)
$V_{c,\text{max}}$	Maximum RuBP saturated rate of carboxylation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
$V_{c,\text{max},T}$	$V_{c,\text{max}}$ corrected to temperature T
W_c	Rubisco limited rate of carboxylation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
W_j	RuBP-limited rate of carboxylation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
α_b	Leaf absorbance at 464 nm wavelength
α_l	Total leaf absorbance
α_r	Leaf absorbance at 634 nm wavelength
β	Fraction of absorbed quanta reaching PSII (%)
Γ^*	CO ₂ compensation point in the absence of dark respiration ($\mu\text{mol mol}^{-1}$)
ΔH_a	Energy of activation (kJ mol^{-1})
ΔH_d	Energy of de-activation (kJ mol^{-1})
ΔS	Entropy term ($\text{kJ K}^{-1} \text{mol}^{-1}$)
Θ	convexity term (dimensionless, 0–1)
Θ_{PSII}	convexity term for electron transport rates (dimensionless, 0–1)
Φ_a	Apparent quantum yield of CO ₂ assimilation (dimensionless)
Φ_{PSII}	Quantum yield of PSII (dimensionless)
$\Phi_{\text{PSII},\text{max}}$	Maximum dark-adapted quantum yield of PSII (F_v/F_m ; dimensionless)
$\Phi_{\text{PSII},\text{max},l}$	Maximum light-adapted quantum yield of PSII (dimensionless)

APPENDIX 2

A. Calculation of CO₂ uptake at any given leaf temperature, assuming no acclimation to growth at different temperatures

The following equations allow prediction of the leaf CO₂ uptake with the model of Farquhar *et al.* (1980) for any leaf temperature using the parameterizations developed in this paper and in Bernacchi *et al.* (2001). Use of this model assumes that $V_{c,\text{max}}$, J_{max} , and R_d at 25 $^{\circ}\text{C}$ are known. Alternatively, if estimates are available for other temperatures then these equations may be re-arranged to determine the value at 25 $^{\circ}\text{C}$.

$$A = (1 - \Gamma^*/C_i) \cdot \min\{W_c \cdot W_j\} - R_{d,c}$$

$$W_c = \frac{V_{c,\text{max},T} \cdot C_i}{C_i + K_c(1 + O/K_o)}$$

$$W_j = \frac{J \cdot C_i}{4.5C_i + 10.5\Gamma^*}$$

$$\Gamma^* = \exp^{(19.02 - 37.83/(R \cdot (T_l + 273.15)))}$$

$$R_{d,T} = R_{d,25^{\circ}\text{C}} \cdot \exp^{(18.72 - 46.39/(R \cdot (T_l + 273.15)))}$$

$$K_c = \exp^{(38.05 - 79.43/(R \cdot (T_l + 273.15)))}$$

$$K_o = \exp^{(20.30 - 36.38/(R \cdot (T_l + 273.15)))}$$

$$V_{c,\text{max},T} = V_{c,\text{max},25^{\circ}\text{C}} \cdot \exp^{(26.35 - 65.33/(R \cdot (T_l + 273.15)))}$$

$$J = \frac{Q_2 + J_{\text{max},T} - \sqrt{(Q_2 + J_{\text{max},T})^2 - 4\Theta_{\text{PSII}}Q_2J_{\text{max},T}}}{2 \cdot \Theta_{\text{PSII}}}$$

$$J_{\text{max},T} = J_{\text{max},25^{\circ}\text{C}} \cdot \exp^{(17.57 - 43.54/(R \cdot (T_l + 273.15)))}$$

$$\Theta_{\text{PSII}} = 0.76 + 0.018T_l - 3.7e^{-4T_l^2}$$

$$Q_2 = Q \cdot a_l \cdot \Phi_{\text{PSII},\text{max}} \cdot \beta$$

$$\Phi_{\text{PSII},\text{max}} = 0.352 + 0.022T_l - 3.4e^{-4T_l^2}$$

B. Calculation of CO₂ uptake at any given leaf temperature, assuming the acclimation to growth temperature observed in tobacco

The following alternative equations for $J_{\max, t}$

$$J_{\max, T} = J_{\max, 25^{\circ}\text{C}} \cdot 1.92 \cdot \exp^{(-0.5 \cdot ((T_g - 26.42)/17.97)^2 + ((T_l - 47.04)/19.38)^2)}$$

$$\Theta_{\text{PSII}} = 0.85 \cdot \exp^{(-0.5 \cdot ((T_g - 25.8)/14.84)^2 + ((T_l - 29.2)/17.99)^2)}$$

$$\Phi_{\text{PSII}, \max} = 0.352 + 0.022T_l - 3.4e^{-4}T_l^2$$