Chapter 10

Modeling the Temperature Dependence of C_3 Photosynthesis

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Summary

The steady-state C_3 model of photosynthesis originally developed by Graham Farquhar et al. (1980) and subsequently modified by others describes responses of leaf carbon assimilation to environmental variation. This mechanistic model states that photosynthesis will be limited by the slowest of three biochemical processes: (1) the maximum rate of Rubisco-catalyzed carboxylation, (2) the rate of ribulose 1,5-bisphosphate (RuBP) regeneration via electron transport (J), or (3) the rate of RuBP regeneration via triose phosphate utilization (TPU). Each of these processes is modeled with parameters that have different responses to temperature; therefore accurate temperature functions are vital to model photosynthetic responses accurately, and they are critical to predict plant ecosystem responses to future predicted increases in temperature and CO_2. Temperature functions used for modeling are frequently derived from Arrhenius equations, which describe changes in rate constants with temperature. Rubisco-limited photosynthesis is modeled using five parameters: two describe enzyme kinetics of carboxylation (V_{cmax} and K_c), one accounts for photorespiration (K_o), one for Rubisco specificity for CO_2 vs. O_2 (Γ^*) and one for mitochondrial respiration (R_d). At light saturation and current atmospheric CO_2 concentration, photosynthesis is usually carboxylation-limited. Two of the above parameters, Γ^* and R_d, are also used to model the rate of RuBP regeneration and follow the same temperature functions. The maximum rate of electron transport (J_{max}) is needed to model RuBP regeneration, which is particularly important at sub-saturating irradiance, higher temperatures, or supra ambient CO_2 concentrations, and is estimated by fitting the response of potential electron transport to light. Unlike the parameters that are dependent on the relatively conserved kinetic properties of Rubisco enzyme, electron transport is sensitive to environmental variation and can vary widely even within species. Triose phosphate limitation can occur at high CO_2, low O_2, high irradiance, or low temperature and is generally difficult to anticipate in field based experiments. Finally, consideration should be given to the supply of CO_2 to the site of carboxylation mediated by mesophyll conductance (g_m) when modeling photosynthetic responses to temperature, as g_m has been shown to vary with temperature, among species and growth conditions.

I. Introduction

The steady-state mechanistic model of C_3 photosynthetic carbon assimilation of Farquhar et al. (1980) is fundamental for predicting leaf responses to environmental variation (Long, 1991). This model provides the basis for scaling carbon uptake from leaves to canopies (Wang and Jarvis, 1990; Amthor, 1995; Lloyd and Farquhar, 1996; dePury and Farquhar, 1997; Wittig et al., 2005), ecosystems (Field and Avissar, 1998) and landscapes (Sellers et al., 1996, 1997). The leaf-level photosynthesis model is also a key component of earth system models (Cramer et al., 2001). Photosynthesis provides the ultimate source of energy for all organisms within terrestrial ecosystems, and models are currently available to predict how photosynthesis is altered by change

Abbreviations: A – net CO_2 uptake rate (μmol m^{-2} s^{-1}); c – scaling constant (unitless); $C - CO_2$ concentration (μmol mol^{-1}); $C_c - CO_2$ concentration in the chloroplast (μmol mol^{-1}); $C_i - CO_2$ concentration in the leaf intercellular airspaces (μmol mol^{-1}); g_{bl} – boundary layer conductance (mol m^{-2} s^{-1}); g_m – mesophyll diffusion conductance (mol m^{-2} s^{-1} bar^{-1}); g_s – stomatal conductance (mol m^{-2} s^{-1}); J_{max} – maximum light saturated rate of electron transport (μmol m^{-2} s^{-1}); K_c – Michaelis constant for carboxylation (μmol mol^{-1}); K_o – Michaelis constant for oxygenation (mmol mol^{-1}); O – oxygen concentration (mmol mol^{-1}); Q – photon flux density (μmol m^{-2} s^{-1}); R – universal gas constant (J K^{-1} mol^{-1}); R_d – respiratory CO_2 released via mitochondrial respiration in the light (μmol m^{-2} s^{-1}); $V_{c,max}$ – maximum rate of carboxylation of Rubisco (μmol m^{-2} s^{-1}); $V_{o,max}$ – maximum rate of oxygenation (μmol m^{-2} s^{-1}); ΔH_a – energy of activation (kJ mol^{-1}); ΔH_d – energy of deactivation (kJ mol^{-1}); Γ^* – photosynthetic CO_2 compensation point (μmol mol^{-1}); Φ_{PSII} – the maximum quantum yield of electron transport (unitless); Θ – the convexity of the transition between the initial slope and the plateau of the hyperbola (unitless); Ω – the range of temperature in which J falls to $e^{-1} = 0.36$ from its optimum value (°C); τ – Rubisco specificity factor (unitless).

in the environment. Given the importance of these models, its accuracy over a wide range of environmental conditions is important for predictions of carbon uptake over numerous scales from leaves to the globe. It is particularly critical that models make accurate predictions over a wide temperature range, as temperature is known to influence many aspects of the biochemical and biophysical reactions that determine rates of photosynthesis (Bernacchi et al., 2001). Accurate modeling is particularly important considering the impact anthropogenically-induced atmospheric and climate change is predicted to have on ecosystems around the globe (Solomon et al., 2007).

Both mean temperature and atmospheric CO_2 concentration are expected to continue increasing during the twenty-first century; therefore predicting photosynthetic changes in response to the interactive effects of rising CO_2 concentration and temperature is critical for understanding how best to manage ecosystems and maximize productivity in the future (Brennan et al., 2007). Growing C_3 plants at high temperature generally leads to a temperature acclimation which increases the thermal optimum for photosynthesis (Berry and Björkman, 1980). It is also well known that elevated CO_2 concentration stimulates photosynthesis by increasing the substrate for carboxylation and by competitively inhibiting oxygenation leading to photorespiration. Therefore the predicted increases in CO_2 and temperature over the next century (Solomon et al., 2007) are expected to have a synergistic effect on photosynthesis (Long, 1991).

Despite the extensive validation of the C_3 photosynthesis model, estimates of the biochemical parameters in the model became more limiting as temperatures deviated from 25 °C and, as originally parameterized, model accuracy decreased at higher and lower temperatures (Bernacchi et al., 2001, 2003). A number of studies have been published providing temperature responses for the parameters used in the photosynthesis model (McMurtrie and Wang, 1993; Harley and Baldocchi, 1995; Bernacchi et al., 2001, 2002, 2003), each with their specific strengths and weaknesses. The focus of this chapter is to provide a discussion of how in the photosynthesis model of Farquhar et al. (1980) CO_2 assimilation rate responds to changes in temperature, with emphases on the temperature dependent parameters and the impact temperature has on the supply of CO_2 into the mesophyll. A complete description of the steady-state photosynthesis model was presented previously (Farquhar et al., 1980; Von Caemmerer, 2000), and an excellent review discussing a mechanistic understanding of the temperature responses of photosynthesis already exists (Sage and Kubien, 2007). Further, numerous modeling studies utilizing the photosynthesis models at multiple scales are available (Long, 1991; Harley and Baldocchi, 1995; Sellers et al., 1997; Wittig et al., 2005).

II. Processes Limiting to C_3 Photosynthesis

The C_3 steady-state photosynthesis model of Farquhar et al. (1980), building upon earlier work (Berry and Farquhar, 1978), reasons that photosynthesis will be limited by the slowest of two biochemical processes: (1) the maximum rate of ribulose 1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) catalyzed carboxylation (Rubisco-limited) and (2) the regeneration of RuBP controlled by electron transport rate (RuBP-limited). The model presented by Farquhar et al. (1980) reasoned that the rate of carboxylation could not exceed the minimum of either of these two limitations, although the actual rate would be lower than either of these. Both ADP and $NADP^+$, availability of which is dependent on the dark reactions, are required by the light reactions for the regeneration of ATP and NADPH. As ATP/ADP and NADPH/$NADP^+$ provide a direct linkage between the 'dark' and 'light' reactions, the potential limitation imposed by the Calvin–Benson–Bassham cycle would likely impact both Rubisco- and RuBP-limited photosynthesis equally (e.g. Farquhar and Von Caemmerer, 1982). Therefore, for the purpose of modeling, it is assumed that photosynthesis is limited by only Rubisco or RuBP regeneration (Berry and Farquhar, 1978; Farquhar and Von Caemmerer, 1982; Chapter 9 of this book by Susanne von Caemmerer, Graham Farquhar and Josph Berry). A third limitation to leaf CO_2 uptake rate is the rate of inorganic phosphate release from the utilization of triose

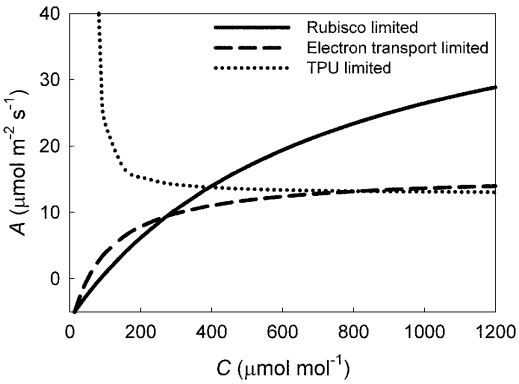

Fig. 10.1. Schematic representation of a photosynthesis (A) vs. CO_2 concentration (C) response curve at saturating light, demonstrating the three potential biochemical/biophysical limitations. Photosynthesis is assumed to operate at whichever limitation gives the lowest rate. At low CO_2 concentrations, the rate is limited by Rubisco, then by electron transport, and at very high CO_2 concentrations by triose phosphate utilization (TPU, dotted line)

phosphates, termed TPU- or P_i-limited photosynthesis (Sharkey, 1985).

The rate of carbon assimilation at any point in time equals the lowest potential rate of the three potential limitations under prevailing environmental conditions, as typically visualized using a photosynthetic CO_2 response curve (Fig. 10.1). We note that when chloroplastic CO_2 concentration is at or below the photosynthetic CO_2 compensation point (Γ^*), this assumption no longer holds. A complexity in modeling photosynthesis is that both CO_2 and O_2 compete for the same active site on Rubisco. Carboxylation of RuBP results in the assimilation of one molecule of CO_2, resulting in two molecules of phosphoglycerate (PGA), which is a precursor to stored or transported carbohydrates. Oxygenation of RuBP, on the other hand, forms one PGA and one phosphoglycolate (PGly) (Bowes et al., 1971; Zelitch, 1971). The formation of PGly initiates photorespiration, where after oxygenation, one CO_2 is eventually released as a by-product (Berry and Farquhar, 1978; Ogren, 1984). Because CO_2 and O_2 compete for the same active site, the mechanistic model of photosynthesis relies on the kinetics of Rubisco regardless of which process limits photosynthesis (Portis, 1992). The complexity associated with the assimilation of CO_2 from photosynthesis and the release of CO_2 from photorespiration is further complicated by simultaneous CO_2 release from mitochondrial respiration in the light (Amthor, 1995). Each of the three processes has parameters that follow different temperature responses, which has traditionally made modeling photosynthesis with temperature difficult (Von Caemmerer, 2000). In the following sections, we will discuss the limiting processes of steady-state leaf photosynthesis with an emphasis on the parameters that are temperature dependent. We will also discuss the temperature functions commonly employed for each of the parameters associated with each limiting process.

A. Rubisco-limited Photosynthesis

The equation describing Rubisco-limited photosynthesis (Farquhar et al., 1980) is:

$$A = \left(1 - \Gamma^*/C\right)\left(\frac{C \cdot V_{c,max}}{C + K_c(1 + O/K_o)}\right) - R_d, \quad (10.1)$$

where Γ^* is the photosynthetic CO_2 compensation point in the absence of mitochondrial respiration (μmol mol^{-1}), C is CO_2 concentration (μmol mol^{-1}), $V_{c,max}$ is the maximum rate of carboxylation of Rubisco (μmol m^{-2} s^{-1}), K_c is the Michaelis constant for carboxylation (μmol mol^{-1}), O is the oxygen concentration (mmol mol^{-1}), and K_o is the Michaelis constant for oxygenation (mmol mol^{-1}). The equation represents Michaelis–Menten kinetics for an enzyme-catalyzed reaction between a substrate, CO_2, and a competitive inhibitor, O_2 (Farquhar et al., 1980) with the term $(1 - \Gamma^*/C)$ representing the proportion of CO_2 that is assimilated relative to the amount of CO_2 that is originally fixed catalytically by Rubisco. Respiratory CO_2 released via mitochondrial respiration in the light is denoted R_d(μmol m^{-2} s^{-1}). Five parameters used in the Rubisco-limited photosynthesis model which represent Rubisco kinetics and mitochondrial respiration (Γ^*, $V_{c,max}$, K_c, K_o, R_d) are temperature dependent, and thus the temperature responses incorporated into the model are critical for model accuracy (Von Caemmerer, 2000).

The terms K_c, K_o and $V_{c,max}$ represent Rubisco enzyme kinetics, and Γ^* is derived from these terms and from the maximum rate of oxygenation ($V_{o,max}$). Kinetic parameters have often

been derived from fits to in vitro data, but in vitro conditions seldom represent those experienced in vivo. For example, changes in temperature have numerous implications for the internal conditions of the leaf, including pH, which can alter the activity of numerous enzymes including Rubisco (Bernacchi et al., 2001). A major challenge associated with in vivo determination of the Rubisco kinetics stems from the limited range of CO_2 in which photosynthesis is Rubisco-limited (Fig. 10.1). The initial portion of the A vs. C response curve corresponds with Rubisco-limited photosynthesis and consists of a range of CO_2 concentrations below the values of K_c and the rates below $0.5V_{c,max}$. When fitting parameters characteristic to the range outside the CO_2 limited one (e.g. $V_{c,max}$), small measurement errors can result in large errors in the derived kinetic parameters (Long and Bernacchi, 2003). This results in statistical challenges, further confounded by the large number of parameters that need to be solved (K_c, K_o, Γ^*, $V_{c,max}$ and R_d).

Despite the complexities associated with solving for the values of the five parameters from the Rubisco-limited photosynthesis, the results have suggested that the Rubisco kinetic parameters (but not V_{max}) are highly conserved among higher plants (Von Caemmerer, 2000; although this may not apply for all C_3 species and for all growth conditions, e.g., Galmés et al., 2005). The term $V_{c,max}$ will vary among leaves within a plant, between plants and among species, even at a standard temperature (Wullschleger, 1993), not speaking about its temperature-dependence. Values will depend on the total number of Rubisco sites active at a given temperature. The number of Rubisco sites is parameterized by the imposition of a particular value of $V_{c,max}$ at a standard reference temperature. A function normalized to unity at the reference temperature will allow for $V_{c,max}$ values to be determined over a wide temperature range from a value measured at a given temperature (Farquhar et al., 1980).

1. The Loss of Rubisco Activity at Higher Temperatures

An idealized curve showing how Rubisco-limited photosynthesis changes with temperature is provided in Fig. 10.2. The mechanism responsible for the observed decline in assimilation above

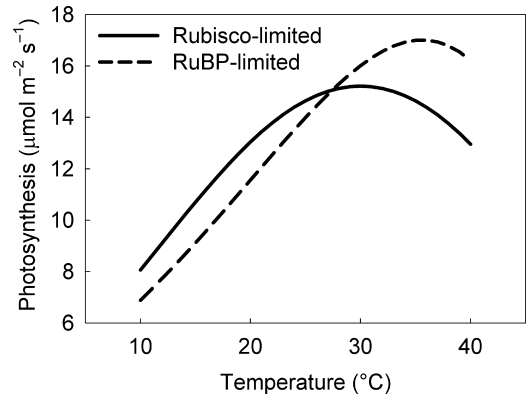

Fig. 10.2. Modeled photosynthetic carbon assimilation plotted as a function of temperature using the Rubisco-limited and the RuBP regeneration-limited photosynthesis model. The curves demonstrate that the rate-limiting process will vary with temperature at constant CO_2 concentration and light intensity. The temperature at which the transition of the rate-limiting process occurs varies (adapted from Kirschbaum and Farquhar, 1984; Cen and Sage, 2005)

the thermal optimum is dual. The first reason is the rapidly increasing affinity for O_2 relative to CO_2 binding to RuBP enediol form in the Rubisco active site (Farquhar et al., 1980). The higher affinity for O_2 results in relatively higher frequencies of oxygenation events at higher temperatures. The second reason is the loss of Rubisco activity due to the deactivation of Rubisco activase at temperatures above the thermal optimum, but below the temperature of enzyme denaturation (Weis, 1981; Kobza and Edwards, 1987; Crafts-Brandner and Salvucci, 2000, 2004; Portis, 2003; Salvucci and Crafts-Brandner, 2004a–c). Whether Rubisco deactivation occurs is currently the focus of debate (Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004a–c; Cen and Sage, 2005; Sage and Kubien, 2007; Sage et al., 2008); however, the implications of this process for modeling photosynthesis at higher temperatures are considered in this chapter.

Most parameters in the Rubisco-limited photosynthesis model (K_c, K_o, Γ^*) are not influenced by changes in the amount or activation state of Rubisco. However, $V_{c,max}$ is linked directly to the number of active Rubisco sites. Thus conditions where Rubisco activity is predicted to decrease, such as supra-optimal temperatures, are critical to model accuracy. Many published datasets provide temperature responses of $V_{c,max}$ using a

variety of techniques (Kirschbaum and Farquhar, 1984; McMurtrie and Wang, 1993; Medlyn et al., 1999; Bernacchi et al., 2001, 2003; Medlyn et al., 2002). If Rubisco is becoming progressively more limiting at temperatures above the thermal optimum as a result of a loss in Rubisco activase stabilization (Eckardt and Portis, 1997), then $V_{c,max}$ will begin to decrease at these temperatures. Of the published datasets, examples exist where $V_{c,max}$ begins to taper off or decrease, although most data suggests that the optimum temperature is reached above 37 °C, if at all (Farquhar, 1979; Harley and Tenhunen, 1991; Harley et al., 1992b; Bernacchi et al., 2001, 2003; Medlyn et al., 2002; Pimentel et al., 2007). A lack of an apparent decrease in Rubisco activity in the in vivo temperature responses provided by Bernacchi et al. (2001, 2002) might be attributed to the antisense construct in the transformant tobacco, which depressed Rubisco content to about 10% of wild-type concentrations without affecting Rubisco activase. In these plants, a 90% loss in the activity of Rubisco activase could therefore occur without affecting the Rubisco activation state. Other published temperature functions of $V_{c,max}$ listed above, as well as the temperature response of $V_{c,max}$ from *Citrus limon* (Fig. 10.3), indicate no decline at temperatures below the temperature at which denaturation of Rubisco occurs.

Although $V_{o,max}$ is shown to increase with temperature, the ratio of $V_{o,max}/V_{c,max}$ declines with temperature, showing that higher temperatures favor an increase in the velocity of carboxylation over oxygenation (Fig. 10.3; Bernacchi et al., 2001). However, the increase with temperature

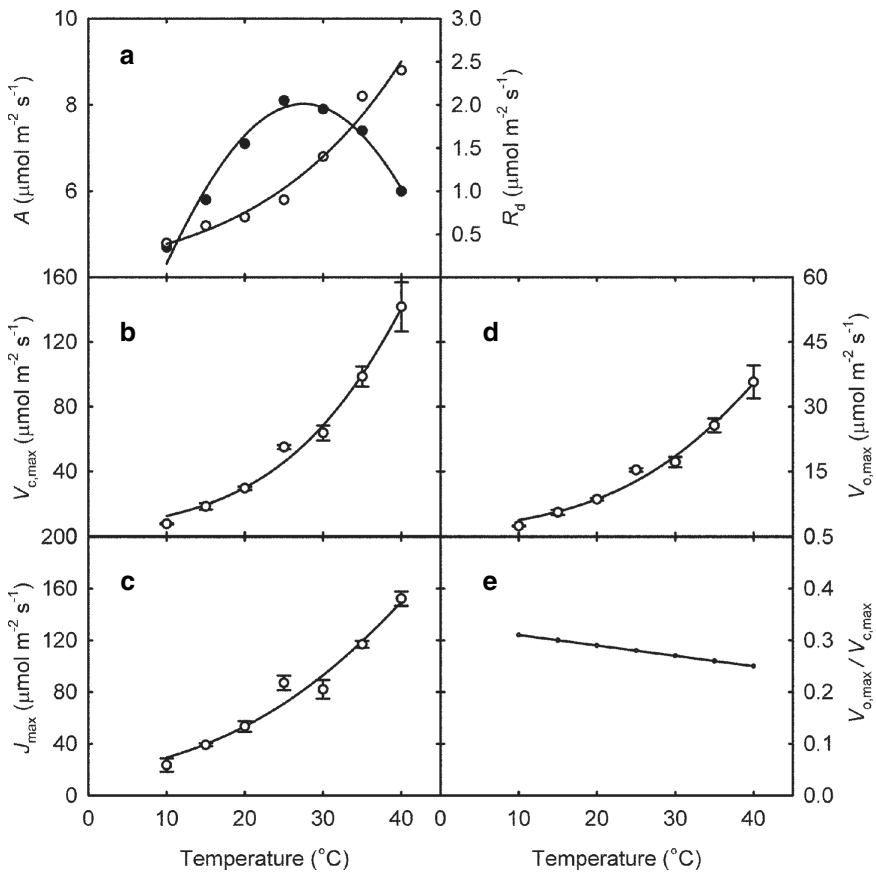

Fig. 10.3. Panel (**a**) shows representative temperature responses of photosynthesis and mitochondrial respiration in the light measured with *Citrus limon*. As a result of photorespiration, the temperature optimum of A is between 25 °C and 30 °C, whereas R_d continues to increase beyond 40 °C. Panels (**b–e**) show the measured temperature responses of $V_{c,max}$ (**b**), $V_{o,max}$ (**c**), J_{max} (**d**), and the ratio of $V_{c,max}$ to J_{max} (**e**). A second order polynomial is fitted to A and Eq. (10.2) is fitted to the other parameters

in maximum rate of carboxylation is offset by changes in affinities of Rubisco for CO_2 and for O_2 (Long, 1991). The Michaelis constant for CO_2 (K_c) increases at a greater rate relative to the Michaelis constant for O_2 (K_o). This results in the affinity for CO_2 increasing slower with temperature than for O_2. The change in the relative enzyme affinities are substantial enough to more than compensate for the increase in $V_{c,max}$ with temperature.

2. Temperature Functions Associated with Rubisco-limited Photosynthesis

The temperature responses of the various model parameters have been described using temperature functions, most commonly Q_{10} (Farquhar et al., 1980), polynomial (Kirschbaum and Farquhar, 1984; McMurtrie and Wang, 1993), exponential (Badger and Collatz, 1977; Harley and Tenhunen, 1991; Bernacchi et al., 2001, 2002, 2003; Medlyn et al., 2002), and the normal distribution (June et al., 2004). Temperature functions for parameters that are based on Rubisco kinetic properties and do not have an optimum are expected to be similar among C_3 species and follow a temperature function which includes only a unitless scaling constant (c) and an energy of activation (ΔH_a, kJ mol^{-1}; Harley and Tenhunen, 1991):

$$Parameter = \exp\left[c - \Delta H_a / RT_k\right], \quad (10.2)$$

where R is the universal gas constant (8.314 J K^{-1} mol^{-1}) and T_k is the leaf temperature (K). This approach simplifies Michaelis constants by assuming that the chemical reactions involved are completely dominated by one rate-limiting step. Equation (10.2) is also standardized to include only ΔH_a (Farquhar et al., 1980; Harley and Baldocchi, 1995):

$$Parameter = Parameter_{25} \exp\left[\frac{(T_k - 298)\Delta H_a}{RT_k 298}\right]. \quad (10.3)$$

Thus, the parameter at 25 °C represents a scaling constant similar to c in Eq. (10.2) and the term $Parameter_{25}$ has associated biological meaning (Harley and Baldocchi, 1995). The significance of ΔH_a in the context of these equations must also be carefully considered. The Michaelis constant is a ratio of the combination of true kinetic constants. The use of an activation energy for it assumes that the 'off' reactions are dominated by a single rate step, which in this case is the formation of product. In situations where a single 'off' step is not dominating the rate, this approach will no longer be strictly applicable. The reverse carboxylation reaction is often thought to be very slow, allowing the temperature expression to be used with confidence. Nevertheless, the approximation probably works reasonably well even when there is significant reverse reaction.

The above Eqs. (10.2 and 10.3) predict that a given model parameter continues to increase exponentially with temperature and that thermal deactivation does not occur. Parameters are often decreasing at higher temperatures and require that the above equations be modified to include energy of deactivation (ΔH_d; kJ mol^{-1}) and an entropy term (ΔS; kJ K^{-1} mol^{-1}) as suggested by Harley and Tenhunen (1991):

$$Parameter = parameter_{25} \frac{\exp\left[c - \Delta H_a / RT_k\right]}{1 + \exp\left[\left(\Delta ST_k - \Delta H_d\right) / RT_k\right]}, \quad (10.4)$$

which again has been further modified to remove the scaling constant, c, as:

$$Parameter = parameter_{opt} \times \frac{H_d \exp\left\{(\Delta H_a / R)\left[\left(1/T_{opt}\right) - (1/T_k)\right]\right\}}{H_d - H_a\left[1 - \exp\left\{(H_a/R)\left[\left(1/T_{opt}\right) - (1/T_k)\right]\right\}\right]}. \quad (10.5)$$

In this latter example, the $parameter_{opt}$ is the value of the parameter at its optimum temperature, (T_{opt}), in which the peak value is achieved. The above examples of temperature functions are not the only functions that have been utilized in determining temperature responses of the model parameters. Unlike polynomials, the functions above are derived from the Arrhenius equations which are based on activation energies.

B. Ribulose 1,5-Bisphosphate (RuBP)-limited Photosynthesis

Light saturation and current ambient CO_2 conditions surrounding the leaf commonly result in photosynthesis being Rubisco-limited. However,

in the natural environment, some leaves are not light-saturated for at least part of the day. For these leaves, the regeneration of RuBP will limit photosynthesis. Temperature is also shown to alter the control of photosynthesis from one limitation to another, and the point of transition varies substantially due to numerous factors (e.g. Fig. 10.2; Cen and Sage, 2005). Additionally, rising atmospheric CO_2 concentration promotes a shift from Rubisco-limited to RuBP-limited photosynthesis, even in saturating light (Fig. 10.1). For these reasons it is equally important to model this limiting process accurately.

It is widely accepted that the regeneration of RuBP is highly dependent on the capacity for electron flow on the chloroplast thylakoid (Evans, 1987; Ögren and Evans, 1993). The RuBP-limited photosynthetic condition of the model of Farquhar et al. (1980) couples RuBP-regeneration to the electron requirements of NADPH and ATP formation, as given by the equation:

$$A = \left(1 - \Gamma^*/C\right)\left(\frac{C \cdot J}{4C + 8\Gamma^*}\right) - R_d. \quad (10.6)$$

The potential of whole chain electron transport (J) is predicted as an empirical hyperbolic function of absorbed photon flux (Q) and the efficiency of photon use (Farquhar and Wong, 1984; Ögren and Evans, 1993). The relationship of J to Q is expressed using a non-rectangular hyperbolic response determined by three parameters: (1) J_{max}, the maximum rate of electron transport, (2) Φ_{PSII}, the maximum quantum yield of electron transport, and (3) Θ, the convexity of the transition between the initial slope and the plateau of the hyperbola (Fig. 10.4). As visualized from Fig. 10.4, the relative importance of these parameters varies with Q: RuBP-limited photosynthesis is more dependent on Φ_{PSII} at lower Q, on Θ at moderate Q, and on J_{max} at higher Q. While the temperature responses of these parameters are critical to modeling accurately RuBP-limited photosynthesis, Φ_{PSII}, and to a lesser extent Θ, is more critical at lower Q where photosynthetic rates are low. Thus, the model is generally less sensitive to errors in these two parameters than those in J_{max}, associated with high photosynthetic rates.

In vitro measurements from isolated thylakoids have been used to estimate J_{max} (Armond et al., 1978; Sage et al., 1995); this technique assumes that the chemical environment of the assay reflects that of the thylakoid, yet large changes occur in vivo that may not be mimicked in vitro. Temperature responses of J_{max} have been determined in vivo from gas-exchange measurements of photosynthesis A vs. leaf intercellular CO_2 concentration C_i (Harley and Tenhunen, 1991; McMurtrie and Wang, 1993; Harley and Baldocchi, 1995; Dreyer et al., 2001; Bernacchi et al., 2003). This method relies on fitting data measured at higher CO_2 concentrations to the RuBP-limited equation for photosynthesis from the Farquhar et al. (1980) model. Estimation of J_{max} from A vs. C_i curves, however, may introduce errors since these curves are often measured at saturating light whereas the photosynthesis model should, in practice, mimic a wide range of conditions, including low light intensities. Model parameterization should also include the possibility that other parameters of the J vs. Q relationship may change with temperature. Changes in these parameters would be especially important when modeling light-limited photosynthesis. Most parameterizations assume Φ_{PSII} to remain constant at 0.85 and the convexity of the transition of J from low to high $Q(\Theta)$ to remain constant at 0.7 over a range of temperatures (Farquhar et al., 1980). Advances in gas exchange and fluorescence measurement techniques provided the opportunity to directly measure temperature responses of the parameters required to model RuBP-limited photosynthesis (Bernacchi et al., 2003). These methods provide

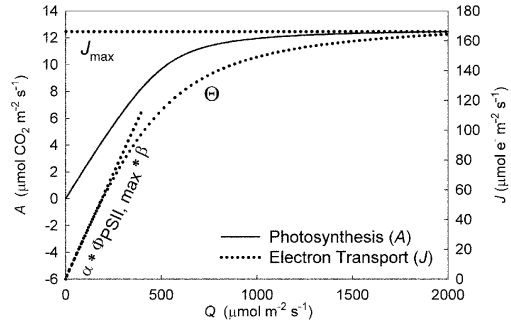

Fig. 10.4. Representation of the parameters required for modeling RuBP regeneration-limited photosynthesis, based on the response of electron transport (J) to incident photon flux (Q). As α and $\Phi_{PSII,max}$ are dominant parameters at low light (thus low rates of photosynthesis), the model is less sensitive to errors associated with these than with J_{max}

simultaneous yet independent measurements of carbon assimilation and electron transport through the thylakoid. Since the RuBP-limited model of photosynthesis predicts the rate of regeneration of RuBP based on the electron requirements for converting NADP to NADPH and ADP to ATP, the temperature responses of Φ_{PSII} and of Θ should be based on the relationship of J to Q (Bernacchi et al., 2003) rather than being derived from A vs. Q response curves (but see Cen and Sage, 2005).

1. Temperature Acclimation of RuBP-limited Photosynthesis

Unlike the parameters associated with the Rubisco-limited photosynthesis model, which are highly dependent on enzyme kinetics and generally conserved among C_3 plants, the parameters associated with the RuBP-limited photosynthesis model, particularly J_{max}, can be highly variable for different C_3 species (Wullschleger, 1993) and for growth conditions, particularly temperature (Sage et al., 1995; Kitao et al., 2000; Von Caemmerer, 2000; Bernacchi et al., 2003; June et al., 2004). The mechanisms behind temperature acclimation of RuBP-limited photosynthesis likely involve changes in thermostability of thylakoid reactions (Berry and Björkman, 1980; Haldimann and Feller, 2005) driven by changes in membrane lipid composition (Raison et al., 1982; Mikami and Murata, 2003) and the possibility that certain Calvin–Benson–Bassham cycle enzymes (e.g. fructose 1,6-bisphosphatase) become limiting under certain circumstances (Badger et al., 1982; Hikosaka et al., 2006). While the mechanisms of acclimation of photosynthesis to temperature (Sage and Kubien, 2007), nutrients (June et al., 2004), and growth irradiance (Von Caemmerer and Farquhar, 1981) are discussed in detail elsewhere, it is critical to consider the variability these factors might induce on the temperature response of the parameters used to model RuBP-limited photosynthesis.

2. Temperature Functions Associated with RuBP-limited Model

Two parameters, Γ^* and R_d, are associated with Rubisco- as well as with RuBP-limited photosynthesis, and as such, their temperature responses are identical whether they are used to model Rubisco- or RuBP-limited photosynthesis. The maximum potential electron transport rate at a particular irradiance ("potential" because it may exceed the actual electron transport rate when the assimilation rate is Rubisco-limited) is critically important for modeling RuBP-limited photosynthesis. As stated above, it is dependent on Φ_{PSII} and to some extent on J_{max} and Θ. Of these three parameters, J_{max} is the most critical for accurate modeling of high rates of photosynthesis, while errors in Φ_{PSII} and Θ can influence model predictions at relatively low light-limited rates of photosynthesis, having little impact on model output. Despite that, temperature responses have been published for both Φ_{PSII} and Θ in tobacco (Bernacchi et al., 2003). The results from this study show that Φ_{PSII} changes only with temperatures below 25 °C and is not altered by growth temperature, whereas Θ is temperature dependent over larger temperature ranges, also acclimating to growth temperature.

Many studies have provided temperature responses of J_{max} using a variety of different methods. While the number of equations used to describe the temperature response of J_{max} under varying growth conditions are many (Harley and Tenhunen, 1991; McMurtrie and Wang, 1993; Ögren and Evans, 1993; Von Caemmerer, 2000; Dreyer et al., 2001; Ziska, 2001; Bernacchi et al., 2003), a simple equation has been presented, accounting for the variation imposed by altered growth conditions (June et al., 2004). The equation expresses the rate of electron transport at a given temperature, $J(T_L)$, as:

$$J(T_L) = J(T_{opt}) e^{-\left(\frac{T_L - T_{opt}}{\Omega}\right)^2}, \qquad (10.7)$$

where $J(T_{opt})$ is the rate of electron transport at the optimum temperature, T_{opt}, and Ω is the range of temperature in which J falls to e^{-1} from its optimum value (June et al., 2004). While this temperature function has been shown to fit numerous published datasets, varying the parameters $J(T_{opt})$, T_{opt} and Ω within species and individual leaves provides the temperature response of J at high irradiance, but not of J_{max}. Simple equations have been employed to estimate J_{max} from J derived from Eq. (10.7) at a given irradiance (Farquhar and Wong, 1984; Ögren and Evans, 1993; Von Caemmerer, 2000; Bernacchi

et al., 2003). More experiments are needed to see whether Eq. (10.7) would also apply to J_{max} directly.

C. Triose Phosphate Utilization (TPU)-limited Photosynthesis

Certain conditions result in photosynthesis being limited by the export and utilization of triose phosphate from the Calvin–Benson–Bassham cycle (Sharkey, 1985; Harley and Sharkey, 1991). This limiting process, termed triose phosphate utilization limited (TPU-limited) photosynthesis, most commonly occurs at high CO_2, low O_2, high irradiance, and/or low temperatures. Triose phosphates created during photosynthesis are mainly converted into starch in the chloroplast or exported into the cytosol and metabolized to sucrose (Leegood, 1996). As triose phosphates are utilized in the chloroplast, inorganic phosphate molecules are released and reused in photophosphorylation. Similarly, when triose phosphates are exported from the chloroplast, they are exchanged 1:1 with inorganic phosphate (Flügge et al., 2003). In cases where sugar phosphates are produced at rates higher than they are consumed, the pool of inorganic phosphate within the chloroplast becomes depleted to the level limiting photophosphorylation (Sharkey, 1985; Sharkey et al., 1986; Leegood and Furbank, 1986; Von Caemmerer, 2000). TPU-limited photosynthesis may result in much lower rates of RuBP regeneration than predicted from rates of electron transport using the RuBP-limited model.

The presence of TPU-limited photosynthesis is difficult to detect even under laboratory conditions. As demonstrated in the A vs. C_i response curves for *Citrus limon* (Fig. 10.5), the presence of TPU-limited photosynthesis is apparent at some measurement temperatures, but not at others. Despite similar laboratory conditions other than measurement temperature, TPU-limited photosynthesis is apparent at lower CO_2 for the measurements at 35 °C than for any other measurement temperature. Despite the evidence of TPU-limited photosynthesis in experimental situations, there is little evidence for this limitation in field-based measurements (Reid and Fiscus, 1998; Adam et al., 2000). Since the TPU-limitation usually occurs in conditions that

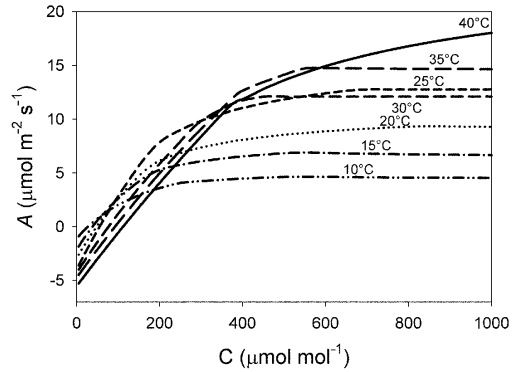

Fig. 10.5. Relationship between photosynthesis (A) and intercellular CO_2 concentration (C_i) for *Citrus limon* measured at temperatures ranging from 10 °C to 40 °C. This dataset demonstrates the influence of rising temperatures on Rubisco-limited (initial slopes), RuBP regeneration-limited (mid to high C_i), and TPU-limited (the highest C_i) photosynthesis. The latter indicates an unpredictable local minimum at 30 °C

are also typical of RuBP-limited photosynthesis (Sharkey, 1985; Harley and Sharkey, 1991), it is often difficult to differentiate between RuBP- and TPU-limited photosynthesis (e.g. Figs. 10.1 and 10.5).

III. Modeling Photosynthesis and the Supply of CO_2

In addition to the biochemical limitations discussed above, carbon supply is also physically limited at the leaf surface (boundary layer conductance g_{bl}), through the stomatal pore (stomatal conductance, g_s), across intercellular air spaces (Nobel, 2005), and from the surface of the mesophyll cells to the chloroplasts. Together, the two latter components are usually termed the 'mesophyll diffusion conductance', g_m. The stomatal conductance, g_s, may increase or remain unchanged in response to temperature changes (Sage and Kubien, 2007), and these responses appear to be independent of photosynthetic biochemistry (Kubien and Sage, 2008). Generally, in the absence of drought and at low leaf-to-air vapor pressure differences, stomatal limitations are largely unchanged at moderately high temperatures (Berry and Björkman, 1980). Modeling photosynthesis without accounting for g_s will overestimate rates of CO_2 uptake to a degree which will vary with environmental conditions.

Another important consideration for modeling photosynthesis is whether to base the model on CO_2 concentration in the leaf intercellular airspaces (C_i) or in the chloroplast (C_c). The importance of using C_i has long been known since g_s responds rapidly to changes in the environment surrounding the leaf (Farquhar and Sharkey, 1982). Historically, it was assumed that the differences between C_i and C_c were sufficiently small and could be ignored (Farquhar and Sharkey, 1982). However, as techniques were developed to address g_m, the conductance associated with the movement of CO_2 from the intercellular airspaces into the chloroplast (Evans et al., 1986; Harley et al., 1992a), it became apparent that g_m could represent a significant limitation to photosynthesis (Evans et al., 1986; Harley et al., 1992a; Loreto et al., 1992; Bernacchi et al., 2002).

Temperature affects various properties associated with cell walls, cytosol, chloroplast membrane, and the stroma, which together constitute g_m (Evans et al., 2004; Loreto et al., 2004; Nobel, 2005). Temperature can also influence the dissolution of CO_2 and its subsequent movement across plasma membranes, which is likely to be influenced by carbonic anhydrase and/or aquaporins (Price et al., 1994; Bernacchi et al., 2002; Terashima and Ono, 2002; Uehlein et al., 2003; Hanba et al., 2004). While the hydration of CO_2 and the following transport of bicarbonate can limit carbon uptake (Price et al., 1994), it appears that membrane transport is the main factor affecting the temperature response of g_m (Uehlein et al., 2003; Hanba et al., 2004).

Measured and estimated values of g_m demonstrate that it varies widely across species and with environmental conditions, but usually it is of sufficient magnitude to significantly affect calculated rates of photosynthesis (Ethier and Livingston, 2004; Warren, 2008). The temperature response of g_m varies across species and growth environments (Bernacchi et al., 2002; Pons and Welschen, 2003; Warren and Dreyer, 2006; Yamori et al., 2006; Diaz-Espejo et al., 2007; Warren et al., 2007). The temperature coefficient (Q_{10}) of g_m is approximately 2.2 for tobacco (Bernacchi et al., 2002), which is consistent with an enzyme-mediated process. Warren and Dreyer (2006) have measured the temperature response of g_m in *Quercus canariensis*: while g_m increased at lower temperatures (from 10 °C to 20 °C), it was stable at higher temperatures (20–35 °C). Similarly, Yamori et al. (2006) showed that g_m increased almost twofold from 10 °C to 20 °C, but changed little at higher temperatures. The range of observed natural variation in g_m indicates that we should be cognizant of its effects when modeling photosynthetic carbon exchange.

Despite the increase in g_m with temperature, the limitation imposed on photosynthesis is shown to increase at higher temperatures (Bernacchi et al., 2002), which suggests the need to incorporate g_m into photosynthesis models. However, this necessity will depend on the objectives for using the model, as parameterizations based either on C_i or on C_c can be employed under different circumstances. Parameterizations based on C_i (e.g. Bernacchi et al., 2001) have changes in g_m confounded with changes in kinetics. It has been shown that photosynthetic capacity and g_m are coupled (Evans and Von Caemmerer, 1996), suggesting that model parameterization based on C_i may be appropriate under conditions where the coupling between g_m and photosynthesis is not expected to change (however the conditions where this assumption applies have not yet been fully elucidated). Modeling exercises where photosynthesis is scaled up from the leaf level may not require incorporation of g_m. However, if the model is employed for determination of V_{cmax} and/or J_{max}, observed differences between treatments may actually be caused by changes in g_m (Ethier and Livingston, 2004).

A. Mitochondrial Respiration

The three processes that limit photosynthesis each dominate under different conditions; however, mitochondrial respiration in the light (R_d) occurs under all conditions and is also shown to be highly temperature dependent (Farquhar et al., 1980; Von Caemmerer, 2000; Bernacchi et al., 2001; Atkin et al., 2005). Whereas the temperature optimum of photosynthesis is generally between 25 °C and 30 °C (as specified above), the temperature optimum of R_d over short timescales (minutes to hours) occurs just below the temperature at which thermal deactivation of enzymes occurs (generally above 42 °C,

e.g. Fig. 10.1). Therefore, modeling photosynthesis at any scale higher than the chloroplast requires that R_d be modeled independently. Traditionally, R_d is considered to follow a temperature function similar to that proposed for many of the photosynthesis parameters, namely that a value at a reference temperature is considered and an exponential function similar to Eq. (10.2) is applied (e.g. Bernacchi et al., 2001). Acclimation of R_d to temperature is shown to occur, and with the acclimation, it has been demonstrated that a generic exponential function normalized to a reference temperature may not represent both the pre- and post-acclimated temperature functions (Atkin et al., 2005). The impact of temperature acclimation of R_d is further complicated by the suppression of mitochondrial respiration in the light, and evidence also exists that changes in CO_2 and O_2 concentrations influence respiratory metabolism (Tcherkez et al., 2008). Despite the need to account for both temperature acclimation and impacts of changes in the environment surrounding the leaf on R_d, a mechanistic understanding – and thus a general model of R_d – is lacking. Therefore, at present, the above-described method in which a relative temperature response is scaled to a value at a reference temperature is utilized.

B. Temperature Parameterizations for the Leaf Photosynthesis Model

There exist a number of datasets providing temperature response functions for models of Rubisco-limited photosynthesis. The original parameterization of the model (Farquhar et al., 1980) incorporated values for the activation energy of $V_{c,max}$, K_c, and K_o based on in vitro Rubisco enzyme activity (Badger and Collatz, 1977). From these values, the temperature response of Rubisco specificity between carboxylation and oxygenation (τ) and of the photosynthetic CO_2 compensation point (Γ^*) were calculated using the relationships:

$$\tau = \frac{V_{c,max} K_o}{K_c V_{o,max}} \tag{10.8}$$

and

$$\Gamma* = \frac{0.5O}{\tau}. \tag{10.9}$$

The temperature responses provided by Badger and Collatz (1977) and a number of additional temperature responses (see Von Caemmerer, 2000) are based purely on in vitro measurements and thus do not accurately mimic the in vivo changes in the leaf which occur over a range of temperatures. Temperature response functions were compiled in the form of a review (McMurtrie and Wang, 1993), although the studies included in the review were also dominated by in vitro measurements.

In vivo kinetics using transgenic tobacco with reduced amounts of Rubisco have been used to determine kinetic constants at 25 °C (Von Caemmerer et al., 1994) and over a biologically significant temperature range (Bernacchi et al., 2001). The benefit of using transgenic tobacco plants for parameterization is that photosynthesis is always limited by Rubisco, allowing for measurements at CO_2 concentrations above those of K_c, approaching $V_{c,max}$. Since the kinetic parameters K_c, K_o and Γ^* are not influenced by the amount of enzyme present, values obtained from these transgenic species are applicable to wild-type plants. The absolute values of $V_{c,max}$ are substantially lower in these transgenic plants; however, the relative temperature response of this parameter is, for the sake of modeling, generally assumed to be similar among higher C_3 species, allowing for these plants to provide more accurate temperature responses for the parameters needed to model Rubisco-limited photosynthesis. The temperature responses derived from these transgenic tobacco plants (Bernacchi et al., 2001) have been validated for a wide range of species.

IV. Concluding Remarks

The response of the net CO_2 uptake rate (A) to temperature is parabolic, and yet the temperature optimum is very plastic and can vary with species, ecotype, site and time of year (Baldocchi and Amthor, 2001). Depending on a wide range of conditions, including temperature, A can be limited by very different processes. The amount and activation state of photosynthetic enzymes, each representing a different limiting process to overall CO_2 assimilation, are integral for determining the temperature optimum of photosynthesis. Each of these limitations needs to be accurately modeled, and thus the temperature

functions accurately represented to provide realistic model output. The C_3 model of photosynthesis (Farquhar et al., 1980) has been used extensively for a variety of purposes, including predicting leaf, canopy, ecosystem, regional and global photosynthesis. The accuracy of the model is dependent on proper parameterization, which includes accurate representation of the parameters over a wide range of temperatures. The parameters incorporated into the model include a range of variables representing enzyme kinetics of Rubisco for both carboxylation and oxygenation as well as variables representing the rate of electron transport for regeneration of RuBP. The supply of CO_2 into the chloroplast, which is frequently temperature dependent, needs to be considered when parameterizing the photosynthesis model. Many parameterizations have been derived from both in vitro and in vivo techniques, with in vivo parameterizations preferred, as it is impossible to mimic the internal environment of the chloroplast in vitro, particularly over a wide range of temperatures.

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