

# Modelling C<sub>3</sub> photosynthesis from the chloroplast to the ecosystem

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## ABSTRACT

**Globally, photosynthesis accounts for the largest flux of CO<sub>2</sub> from the atmosphere into ecosystems and is the driving process for terrestrial ecosystem function. The importance of accurate predictions of photosynthesis over a range of plant growth conditions led to the development of a C<sub>3</sub> photosynthesis model by Farquhar, von Caemmerer & Berry that has become increasingly important as society places greater pressures on vegetation. The photosynthesis model has played a major role in defining the path towards scientific understanding of photosynthetic carbon uptake and the role of photosynthesis on regulating the earth's climate and biogeochemical systems. In this review, we summarize the photosynthesis model, including its continued development and applications. We also review the implications these developments have on quantifying photosynthesis at a wide range of spatial and temporal scales, and discuss the model's role in determining photosynthetic responses to changes in environmental conditions. Finally, the review includes a discussion of the larger-scale modelling and remote-sensing applications that rely on the leaf photosynthesis model and are likely to open new scientific avenues to address the increasing challenges to plant productivity over the next century.**

*Key-words:* modeling, photosynthesis, scaling.

## INTRODUCTION

The plant biology community during the early days of photosynthesis research was met with significant challenges in understanding the processes that determine rates of leaf-level net carbon dioxide assimilation ( $A$ ). These challenges were related to the fact that three metabolic pathways, photosynthesis (PS), photorespiration (PR) and mitochondrial respiration ( $R_d$ ), are all involved in the movement of carbon dioxide into (PS) or out of (PR,  $R_d$ ) a leaf and that two of the pathways (PS, PR) are catalysed by the same enzyme in a competitive

manner. Layered on this complexity is the fact that PS can be limited by the kinetics of the primary carboxylating enzyme, Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco), electron transport-limited rates of RuBP regeneration and/or inorganic phosphate limitation associated with triose phosphate utilization. The mechanistically based leaf photosynthesis model (Farquhar, von Caemmerer & Berry 1980), hereafter referred to as the leaf  $A$  model, brought together the disparate, yet quickly evolving research into an eloquent and mechanistically sound model that addressed photosynthetic carbon uptake under a range of environmental conditions.

The original version of the leaf  $A$  model assumed two limitations; the process that is most limiting coincides with the actual  $A$ . The first limiting process is the initial carboxylation event catalysed by Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). The model assumes that Rubisco-limited  $A$  follows a Michaelis–Menten response function modified to account for a competitive inhibitor, oxygen. As is typical of any Michaelis–Menten reaction, increasing the limiting substrate (CO<sub>2</sub>), the amount of enzyme present (Rubisco), or decreasing the competitive inhibitor (O<sub>2</sub>) will yield higher reaction rates. Therefore, this limiting process has been referred to as Rubisco-, carboxylation- and CO<sub>2</sub>-limited  $A$ ; in this review, the term Rubisco-limited is used. The second limiting process included in the original model (Farquhar *et al.* 1980) is assumed to relate to the rate in which the light reactions generate ATP and NADPH from the precursors ADP and NADP<sup>+</sup>, respectively, for use in the photosynthetic carbon reduction cycle. The rate in which ATP and NADPH are formed is linked directly to the rate of linear electron transport ( $J$ ). Therefore, using the assumed stoichiometry associated with the photosynthetic requirements for ATP and NADPH (reviewed in von Caemmerer 2000),  $A$  is modelled based on rates of  $J$  supported by a given photosynthetically active photon flux density (PPFD). Later, a third limitation was identified, which relates  $A$  to the rate in which inorganic phosphate is released during the utilization of triose-phosphates, termed TPU- or P<sub>i</sub>-limited  $A$  (Sharkey 1985).

The leaf  $A$  model, as indicated by the thousands of citations in peer-reviewed literature, is an extremely useful tool and the relevance of this model has not diminished over time. This model has been used to simulate  $A$  in hierarchical

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modelling schemes that consider larger spatiotemporal scales, including canopies (Wang & Jarvis 1990; Amthor 1994; Lloyd & Farquhar 1996; dePury & Farquhar 1997; Wittig *et al.* 2005; Drewry *et al.* 2010a,b), ecosystems (Field & Avissar 1998) and landscapes (Sellers *et al.* 1996, 1997). The leaf  $A$  model is also a key component of earth system models (Cramer *et al.* 2001; Medvigy *et al.* 2009). With the major challenges facing society in terms of global climate change, a growing population and higher caloric intake, the importance of the leaf  $A$  model as a tool for global change research is increasing. Given this role, the accuracy of the model is important for predicting carbon uptake across spatial scales from leaves to the globe and over time scales ranging from seconds to decades or longer. The importance of the model to accurately predict  $A$  was quickly realized; however, significant advances in technology, including measurement protocols and genetic manipulations (e.g. Bernacchi *et al.* 2001; Yamori & von Caemmerer 2009), were required to provide model parameterizations that adequately model  $A$  over a range of conditions that are biologically significant, including fluctuations in light,  $\text{CO}_2$  and temperature.

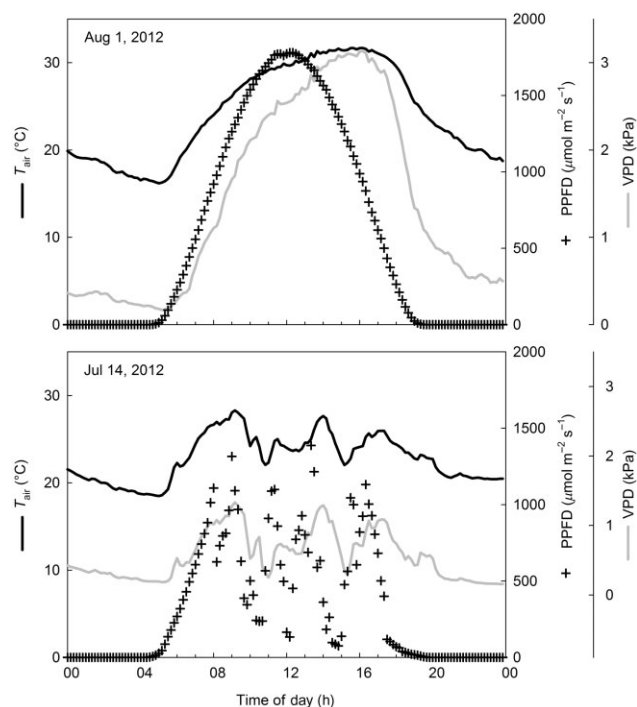
The goals of this review are threefold. Firstly, we will provide a review of the model as it developed from 1980 to its present state, with specific discussion related to the ability of the model to predict  $A$  with changes in temperature and drought, increasing carbon dioxide and ozone, as well as a discussion focusing on the assumptions of the three limiting processes integrated into the model. Secondly, review leaf scale model applications including the fitting of measured data to obtain key photosynthetic parameters, and the potential for the model to identify opportunities to improve photosynthesis. Thirdly, we discuss the role of the leaf  $A$  model in scaling from the leaf to the canopy, with specific focus on canopy and ecosystem models and remote-sensing applications.

## MODELLING LEAF $A$ IN A CHANGING ENVIRONMENT

Because of the mechanistic nature of the leaf  $A$  model, it is a great tool to predict changes in  $A$  over a wide range of environmental conditions. The major environmental determinants of  $A$  include air temperature ( $T_{\text{air}}$ ) and PPFD; these are all highly dynamic in nature (Fig. 1). While changes in vapour pressure deficit (VPD) do not directly influence photosynthetic physiology, it does have a strong influence on stomatal conductance ( $g_s$ ), which is not integrated directly into the model. Not only does the photosynthetic model need to account for short-term (i.e. minutes to hours) fluctuations in environmental conditions, it must also consider the impact of longer-term changes, including anthropogenically induced climate change that is predicted to continue well into the future (Solomon *et al.* 2007).

### Model background

A complete description of the leaf  $A$  model was presented previously (Farquhar *et al.* 1980; Farquhar & von Caemmerer 1982; von Caemmerer 2000); however, the key modelling



**Figure 1.** Meteorological conditions measured at a research station in Central Illinois during a clear (top) and overcast (bottom) day in 2012.

equations are presented here to aid in the discussion of proper model parameterization. The basic model predicts  $A$  as a function of three separate processes that are involved in the flux of  $\text{CO}_2$  into or out of the leaf as

$$A = V_c - 0.5V_o - R_d, \quad (1)$$

where  $V_c$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is the rate of carboxylation by Rubisco,  $V_o$  ( $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is the rate of oxygenation by Rubisco and  $R_d$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) is the rate of mitochondrial release of  $\text{CO}_2$ . The stoichiometry of PR assumes that for two oxygenations of Rubisco, one  $\text{CO}_2$  is released; thus, the multiplier of 0.5 is associated with  $V_o$ . Because the carboxylation and oxygenation reactions share the same active site on Rubisco, the PS and PR components of the model are expressed as

$$A = \left(1 - \frac{\Gamma^*}{C}\right)V_c - R_d. \quad (2)$$

The term  $C$  is the concentration of  $\text{CO}_2$  ( $\mu\text{mol mol}^{-1}$ ) and the term  $\Gamma^*$  ( $\mu\text{mol mol}^{-1}$ ) is the photosynthetic  $\text{CO}_2$  compensation point, the concentration at which photosynthetic carbon uptake is equal to photorespiratory  $\text{CO}_2$  release. The full derivation of  $(1 - \Gamma^*/C)$  is outside the scope of this review; however,  $\Gamma^*/C$  represents the proportion of  $\text{CO}_2$  taken up by PS ( $V_c$ ) that is released by PR.

The photosynthetic  $\text{CO}_2$  compensation point,  $\Gamma^*$ , is a value that is based on the specificity of Rubisco for  $\text{CO}_2$  compared with  $\text{O}_2$  ( $\tau$ ), expressed as

$$\Gamma^* = \frac{0.5 \cdot O}{\tau}, \quad (3)$$

where  $O$  ( $\text{mmol mol}^{-1}$ ) is the concentration of  $\text{O}_2$ . The value of  $\tau$  is relatively constant among  $\text{C}_3$  species (von Caemmerer 2000); however, the extent to which it varies may need to be considered depending on the model application (Galmés *et al.* 2005). Specificity is a function of the kinetics of Rubisco, given by

$$\tau = \left( \frac{K_o V_{c,\max}}{V_{o,\max} K_c} \right) \quad (4)$$

where  $K_c$  and  $K_o$  are the Michaelis constants, and  $V_{c,\max}$  and  $V_{o,\max}$  are the maximum velocities of carboxylation and oxygenation of Rubisco, respectively.

An additional challenge associated with modelling  $V_c$  stems from the various processes that limit  $A$ , Rubisco ( $w_c$ ), RuBP regeneration ( $w_j$ ) and TPU ( $w_p$ ). These limiting processes are most commonly presented based on the carbon dioxide concentration ( $[\text{CO}_2]$ ) where they limit (Fig. 2; <http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToCarbonDioxide/>).  $V_c$  is represented as the minimum of these three processes ( $V_c = \min\{w_c, w_j, w_p\}$ ), each described mathematically as

$$w_c = \frac{V_{c,\max} \cdot C}{C + K_c(1 + O/K_o)}, \quad (5)$$

$$w_j = \frac{J \cdot C}{4.5C + 10.5\Gamma^*}, \quad (6)$$

$$w_p = \frac{3TPU}{(1 - \Gamma^*/C)}. \quad (7)$$

The term  $J$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) represents the flux of electrons through the thylakoid membrane and TPU is the rate of triose phosphate utilization ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).  $J$  is a function of the maximum potential electron transport rate ( $J_{\max}$ ), the PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), the ratio of photosystem II (PSII) to photosystem I (PSI,  $\beta$ ), leaf absorbance ( $\alpha$ ), quantum efficiency of PSII ( $\Phi$ ) and a curvature term ( $\Theta$ ), expressed as a quadratic equation as

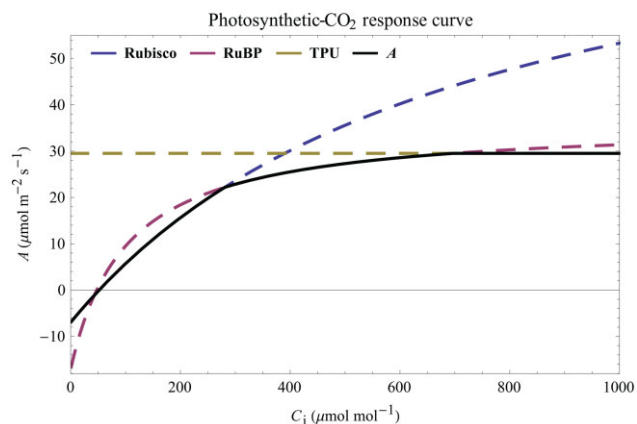
$$J = \frac{PPFD\alpha\Phi\beta + J_{\max} - \sqrt{(PPFD\alpha\Phi\beta + J_{\max})^2 - 4\Theta PPFD\alpha\Phi\beta J_{\max}}}{2\Theta}. \quad (8)$$

Given the mechanistic nature of the leaf  $A$  model, its ability to accurately reflect the responses of  $A$  relies on proper parameterization of key terms used in the model (Table 1). The parameters are all highly temperature dependent and can be determined from a number of different sources (e.g. Bernacchi *et al.* 2001, 2002; Medlyn, Loustau & Delzon 2002; Bernacchi, Pimentel & Long 2003a; Hikosaka *et al.* 2006). The temperature responses of the model parameters have been described using a variety of functions, most commonly  $Q_{10}$  (Farquhar *et al.* 1980), polynomial (Kirschbaum & Farquhar 1984; McMurtrie & Wang 1993), exponential (Badger & Collatz 1977; Harley & Tenhunen 1991; Bernacchi *et al.* 2001, 2002, 2003a; Medlyn *et al.* 2002; Kattge & Knorr 2007) and a normal distribution (June, Evans & Farquhar 2004). Temperature functions for parameters that are based on Rubisco kinetic properties and do not have an optimum within a biologically significant temperature range ( $K_c$ ,  $K_o$ ,  $\tau$ ,  $\Gamma^*$  and in most cases  $V_{c,\max}$ ) follow a temperature function that includes only a unitless scaling constant ( $c$ ) and an energy of activation ( $\Delta H_a$ ;  $\text{kJ mol}^{-1}$ ):

$$Parameter = \exp[c - \Delta H_a / RT_k], \quad (9)$$

where  $R$  is the universal gas constant ( $8.314 \text{ J K}^{-1} \text{ mol}^{-1}$ ) and  $T_k$  is the leaf temperature (K). Equation 9 is derived originally from the Eyring equation (Eyring 1935) through the work of Johnson & Lewin (1946) and adapted to the temperature functions of  $A$  by Harley & Tenhunen (1991). Equation 9 can also be standardized to include only  $\Delta H_a$  (Farquhar *et al.* 1980; Harley & Baldocchi 1995) as

$$Parameter = Parameter_{25} \exp\left[\frac{(T_k - 298)\Delta H_a}{RT_k 298}\right]. \quad (10)$$



**Figure 2.** An idealized  $A/C_i$  response curve modelled at  $25^\circ\text{C}$  and photosynthetic photon flux density (PPFD) of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  using the leaf  $A$  model (Farquhar *et al.* 1980) with the temperature functions for Rubisco- and RuBP regeneration-limited  $A$  provided in Bernacchi *et al.* (2001, 2003a) with the temperature response of  $J_{\max}$  modified as in June *et al.* (2004) and the temperature response of TPU-limited  $A$  from Harley *et al.* (1992). Modelled  $A$  is determined by whichever process is the most limiting (solid black line) with the functions representing non-limiting portions of the three processes shown in the dashed lines. This figure was modelled using  $V_{c,\max}$  of  $98 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $J_{\max}$  of  $160 \mu\text{mol m}^{-2} \text{s}^{-1}$ , TPU of  $10.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $R_d$  of  $1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ . This figure can be manipulated over a wide range of conditions and parameterizations at: <http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToCarbonDioxide/>

**Table 1.** Symbols, definitions, units and whether the term is calculated in the model or input as a parameter

Symbol	Definition	Units	Input/Parameter/Output
$A$	Net CO <sub>2</sub> assimilation rate	$M\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$C$	CO <sub>2</sub> concentration	$\mu\text{mol mol}^{-1}$	Input
$J$	Electron transport rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$J_{\text{max}}$	Maximal electron transport rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Parameter
$K_c$	Michaelis constant for CO <sub>2</sub>	$\mu\text{mol mol}^{-1}$	Parameter
$K_o$	Michaelis constant for O <sub>2</sub>	$\text{mmol mol}^{-1}$	Parameter
$O$	O <sub>2</sub> concentration	$\text{mmol mol}^{-1}$	Input
$R_D$	Mitochondrial respiration in the light	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Parameter
TPU	Triose phosphate utilization rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Parameter
$V_c$	Carboxylation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$V_{c,\text{max}}$	Maximal carboxylation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Parameter
$V_o$	Oxygenation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$V_{o,\text{max}}$	Maximal oxygenation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Parameter
$w_c$	Rubisco-limited carboxylation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$w_j$	RuBP-limited carboxylation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$w_p$	TPU-limited carboxylation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Calculated
$\alpha$	Leaf absorbance	–	Parameter
$\beta$	Fraction of photosystem II to photosystem I	–	Parameter
$\Gamma^*$	Photosynthetic CO <sub>2</sub> compensation point	$M\text{mol mol}^{-1}$	Parameter
$\Theta$	Curvature term	–	Parameter
$\tau$	Rubisco specificity for CO <sub>2</sub> versus O <sub>2</sub>	–	Parameter
$\Phi$	Quantum efficiency of photosystem II	–	Parameter
PPFD	Photosynthetic photon flux density	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Input

Here, the parameter at 25 °C ( $Parameter_{25}$ ) represents a scaling constant similar to  $c$  in Eqn 9 and therefore has intuitive biological meaning (Harley & Baldocchi 1995).

Equations 9 and 10 predict that a given model parameter continues to increase exponentially with temperature and that thermal deactivation does not occur. However, several model parameters display a decrease at higher temperatures and require an energy of deactivation ( $\Delta H_d$ ;  $\text{kJ mol}^{-1}$ ) and an entropy term ( $\Delta S$ ;  $\text{kJ K}^{-1} \text{mol}^{-1}$ ) to account for loss of enzyme function above a certain energy level. These terms are integrated into Eqn 9 as (Harley & Tenhunen 1991)

$$Parameter = \frac{\exp[c - \Delta H_a / RT_k]}{1 + \exp[(\Delta ST_k - \Delta H_d) / RT_k]}, \quad (11)$$

which again has been further modified to remove the scaling constant,  $c$  (as in Harley & Baldocchi 1995):

$$Parameter = parameter_{\text{opt}} \frac{H_d \exp\{(\Delta H_a / R)[(1/T_{\text{opt}}) - (1/T_k)]\}}{H_d - H_a [1 - \exp\{(H_a / R)[(1/T_{\text{opt}}) - (1/T_k)]\}]}. \quad (12)$$

In this later example, the  $parameter_{\text{opt}}$  is the peak value of the parameter and  $T_{\text{opt}}$  is the temperature in which this peak occurs. Examples of temperature functions extend beyond those presented here. However, functions derived from the Arrhenius equations, which are based on activation energies, are among the most widely employed.

## MODEL PARAMETERIZATION: RUBISCO-LIMITED A

The key parameters used in the Rubisco-limited  $A$  model include  $K_c$ ,  $K_o$  and  $V_{c,\text{max}}$ , which represent Rubisco enzyme kinetics, and  $\Gamma^*$ , which is derived from these three terms and from the maximum rate of oxygenation ( $V_{o,\text{max}}$ ; Eqns 3 and 4). Each of these kinetic components of Rubisco is highly temperature dependent; therefore, the model's predictive ability depends on accurately representing the temperature responses of these parameters. The original model (Farquhar *et al.* 1980) utilized temperature responses that were derived from isolated Rubisco using *in vitro* techniques (Badger & Collatz 1977). However, *in vitro* conditions seldom represent those experienced *in vivo*. *In vitro* assays are usually conducted under dilute conditions relative to the *in vivo* situation where the active site concentrations can range above 1 mM (Jensen & Bahr 1977; von Caemmerer *et al.* 1994). A major challenge associated with *in vivo* determination of the Rubisco kinetics included, originally, accurate methods for measuring gas-exchange coupled with the limited range and low values of  $[\text{CO}_2]$  in which  $A$  is Rubisco-limited. Rubisco-limited  $A$  occurs at  $[\text{CO}_2]$  below the value of  $K_c$  (ca.  $400 \mu\text{mol mol}^{-1}$  based on intercellular  $[\text{CO}_2]$ ,  $C_i$ ); thus, small measurement errors can result in large errors in the derived kinetic parameters (Long & Bernacchi 2003). This small  $[\text{CO}_2]$  range in which  $A$  is Rubisco-limited and the large number of dependent model parameters (e.g.  $K_c$ ,  $K_o$ ,  $\Gamma^*$ ,  $V_{c,\text{max}}$  and  $R_d$ ) presents a challenge to proper model parameterization. Improvements in *in vivo* measurement techniques (e.g. newer generation gas-exchange systems and chlorophyll fluorometers) together with antisense technology, in which

plants are engineered with low Rubisco content to ensure PS is always Rubisco-limited (von Caemmerer *et al.* 1994), has paved the way for the development of improved temperature response functions that are statistically valid with enhanced accuracy (e.g. Bernacchi *et al.* 2001).

It is typically assumed that the kinetic parameters associated with Rubisco-limited  $A$  were conserved for all higher  $C_3$  species (Farquhar *et al.* 1980; Harley & Tenhunen 1991; von Caemmerer 2000; Bernacchi *et al.* 2001; Long & Bernacchi 2003), although this may not apply for all  $C_3$  species and for all growth conditions (e.g. Galmés *et al.* 2005). The degree to which assuming a default model parameterization is appropriate ultimately depends upon the intended purpose for modelling  $A$ . Certain parameters must be known or fixed for a leaf to ensure that error is minimized. Improper parameterization of  $V_{c,max}$  can introduce errors in modelled photosynthetic rates that are far greater than those associated with incorrect Rubisco kinetic values (e.g.  $\tau$ ). Because  $V_{c,max}$  varies among leaves within a plant, with leaf age, between plants, among species and seasonally (Wilson, Baldocchi & Hanson 2000b; Medlyn *et al.* 2002; Xu & Baldocchi 2003; Niinemets *et al.* 2006; Kattge *et al.* 2009), even at a standard temperature (Wullschleger 1993), there is considerable potential to introduce significant error in modelled photosynthetic rates. The values of  $V_{c,max}$  will depend on the total number of Rubisco reaction sites present (Rubisco content) and active (Rubisco activation) under a given set of circumstances. Given its highly variable nature,  $V_{c,max}$  is considered a model input and if specific experimental values cannot be obtained from the system being modelled, values specific to the species of interest can be taken, with caution, from the literature. The temperature response of  $V_{c,max}$ , however, is conserved among  $C_3$  plants; thus, it is normalized to one at a reference temperature (25 °C in Bernacchi *et al.* 2001, 2003a). Some evidence shows that the temperature response of  $V_{c,max}$  might vary with species or plant functional type (PFT) (e.g. Medlyn *et al.* 2002; Hikosaka *et al.* 2006). Despite the uncertainty surrounding proper parameterization, the temperature functions provided using tobacco (Bernacchi *et al.* 2001, 2003a) have been used extensively to accurately model a wide range of PFTs in a range of environmental conditions.

### Model parameterization: RuBP regeneration-limited

The parameters  $I^*$  and  $R_1$  are associated both with Rubisco- and RuBP regeneration-limited  $A$ , and as such, the same temperature response for each respective parameter is used for modelling both processes. The potential electron transport rate at a particular irradiance ( $J$ ; 'potential' because it may exceed the actual electron transport rate when the assimilation rate is Rubisco-limited) is critically important for modelling RuBP regeneration-limited  $A$ . Of the parameters used to model  $J$  (Eqn 8), the model is most sensitive to the maximum potential electron transport rate ( $J_{max}$ ) when photosynthetic rates are highest – relatively warm temperature, ample light – whereas  $\Phi$  and  $\Theta$  are more influential at a relatively low light-limited  $A$ .

Many studies have provided temperature responses of  $J_{max}$  using a variety of different methods and in a wide range of growth conditions (Harley & Tenhunen 1991; McMurtrie & Wang 1993; Ögren & Evans 1993; von Caemmerer 2000; Dreyer *et al.* 2001; Ziska 2001; Bernacchi *et al.* 2003a). However, June *et al.* (2004) presented a simple formulation that can account for the variation imposed by altered growth conditions by expressing  $J$  at a given temperature,  $J(T_L)$ , as

$$J(T_L) = J(T_{opt}) e^{-\left(\frac{T_L - T_{opt}}{\Omega}\right)^2}, \quad (13)$$

where  $J(T_{opt})$  is the rate of electron transport at the optimum temperature,  $T_{opt}$ , and  $\Omega$  is the range of temperature in which  $J$  falls to  $e^{-1}$  from its optimum value (June *et al.* 2004). Importantly, this temperature function has been shown to fit numerous published datasets (June *et al.* 2004), which allows for standardization of the model form. The key parameters  $J(T_{opt})$ ,  $T_{opt}$  and  $\Omega$  vary among leaves, individuals and species; thus, they should be determined through measurements. The  $J$  determined using this approach represents the rate of electron transport at any given temperature based on the PPFD in which the measurements were made. Because  $J_{max}$  at a reference temperature is highly variable, and it is often impractical to determine  $J(T_{opt})$ ,  $T_{opt}$  and  $\Omega$  from Eqn 13 for each leaf of interest, the equation can be normalized to 1 at 25 °C, allowing for  $J_{max}$  measured at this reference temperature to be incorporated into the model as

$$J(T_L) = J_{max,25^\circ C} \frac{e^{-\left(\frac{T_L - T_{opt}}{\Omega}\right)^2}}{e^{-\left(\frac{25 - T_{opt}}{\Omega}\right)^2}}, \quad (14)$$

where  $J_{max,25^\circ C}$  is  $J_{max}$  measured at 25 °C. Values for  $T_{opt}$  and  $\Omega$  are also likely to change based on growth conditions surrounding the leaf; however, generalized values for some species have been provided elsewhere (June *et al.* 2004). Relatively simple equations have been employed to estimate  $J$  from a known  $J_{max}$  at any PPFD (Farquhar & Wong 1984; Ögren & Evans 1993; von Caemmerer 2000; Long & Bernacchi 2003; June *et al.* 2004).

The notion that the regeneration of RuBP is limited by  $J$  is questionable. The success of the leaf  $A$  model suggests that  $J$  is involved to a large extent; however, the temperature dependence of  $J_{max}$  is significantly more variable than has been observed for any other parameter in the model (Wullschleger 1993; Sage, Santrucek & Grise 1995; Kitao *et al.* 2000; von Caemmerer 2000; Bernacchi *et al.* 2003a; June *et al.* 2004). The mechanisms behind temperature acclimation of RuBP regeneration-limited  $A$  likely involve changes in thermostability of thylakoid reactions (Berry & Björkman 1980; Haldimann & Feller 2005) that are driven by changes in membrane lipid composition (Raison, Pike & Berry 1982; Mikami & Murata 2003). It is also possible that certain photosynthetic carbon reduction (PCR) cycle enzymes (e.g. fructose-1,6-bisphosphatase) become limiting under certain circumstances (Badger, Björkman & Armond 1982; Hikosaka *et al.* 2006). For example, genetic engineering of plants that express higher concentrations of the PCR cycle

enzyme sedoheptulose biphosphatase (SBPase) is shown to increase  $A$  in tobacco, suggesting that this PCR cycle enzyme is limiting at least under some conditions (Lefebvre *et al.* 2005). While the mechanisms of acclimation of  $A$  are discussed in detail elsewhere (June *et al.* 2004; Sage & Kubien 2007), it is critical to consider the influence of growth conditions when modelling RuBP regeneration-limited  $A$ .

### Model parameterization: TPU-limited

The third process that limits  $A$  relates to the export and utilization of triose phosphate (Sharkey 1985; Harley & Sharkey 1991). Triose phosphates created during PS are mainly converted into starch in the chloroplast or exported into the cytosol and metabolized to sucrose (Leegood 1996). Within the chloroplast, inorganic phosphate molecules are released as triose phosphates and reused in photophosphorylation. When triose phosphates are exported from the chloroplast, they are exchanged with inorganic phosphate (Flügge *et al.* 2003). The higher production rates of sugar phosphates can deplete the pool of free inorganic phosphate and limit photophosphorylation (Sharkey 1985; Leegood & Furbank 1986; Sharkey *et al.* 1986; von Caemmerer 2000). This limiting process, termed triose phosphate utilization limited (TPU-limited)  $A$ , occurs primarily at high  $\text{CO}_2$  (Sage 1994), high irradiance (Sharkey 1985) and/or low temperatures (Labate & Leegood 1988). TPU-limited  $A$  result in much lower rates of RuBP regeneration than predicted from rates of electron transport using the RuBP regeneration-limited model.

The challenges in detecting TPU-limited  $A$  make this process the most difficult to model. Despite the evidence of TPU-limited  $A$  in experimental situations, the evidence for this limitation in field-based measurements is sparse. As the TPU-limitation usually occurs in conditions that are typical of RuBP regeneration-limited  $A$  (Sharkey 1985; Harley & Sharkey 1991), it is often difficult to differentiate between RuBP regeneration- and TPU-limited  $A$ . These difficulties have resulted in few published functions describing how TPU changes with temperature, although a function determined for cotton (Harley *et al.* 1992) is presented elsewhere in this review.

## MODEL APPLICATIONS

As described previously (Farquhar, von Caemmerer & Berry 2001), the leaf  $A$  model has been used for three main purposes; pedagogical, extrapolating key parameters associated with physiological significance (e.g.  $V_{c,\max}$  for Rubisco content/activation,  $J_{\max}$ ,  $R_d$ ) from measurements and scaling. Advances in remote-sensing techniques, the need for increasing crop productivity, and refinement of model predictions at canopy, ecosystem, biome and global levels for global carbon cycle science have elevated the role of the model, with accurate parameterizations, beyond its initial range of applications. These will be discussed in this section. Unless stated otherwise, the temperature functions integrated into the leaf model are taken from Bernacchi *et al.* (2001) for the temperature responses of Rubisco-limited  $A$ , from Bernacchi

*et al.* (2003a) but using the temperature response function for  $J_{\max}$  from June *et al.* (2004) for RuBP regeneration-limited  $A$  and from Harley *et al.* (1992) for TPU-limited  $A$ .

### Using the model to fit data

A major use of the leaf  $A$  model lies in the equations used to fit measured data in order to extract the physiologically meaningful variables  $V_{c,\max}$  and  $J_{\max}$ , and to a lesser extent  $R_d$ ; accurate determination of foliar respiration generally requires detailed measurement techniques beyond the scope of most global change studies (e.g. Leakey *et al.* 2009; Gillespie *et al.* 2012). The purpose of photosynthetic model fitting varies; in some cases,  $V_{c,\max}$  and  $J_{\max}$  are used as inputs for modelling exercises (as described earlier), whereas in other cases, the parameters are used to describe physiological responses of leaves to different treatments (e.g. Ainsworth *et al.* 2002; Centritto 2002; Bernacchi *et al.* 2003a, 2005). Photosynthetic carbon assimilation versus  $[\text{CO}_2]$  response curves based on intercellular ( $A-C_i$ ) or chloroplastic ( $A-C_c$ )  $[\text{CO}_2]$  are needed regardless of the technique used to fit the data to the model.

Among the numerous methods employed and tested (e.g. Miao *et al.* 2009; Zeng *et al.* 2010), the most common method relies on separate fitting for the Rubisco- and RuBP regeneration-limited  $A$  (e.g. Bernacchi *et al.* 2003b, 2005; Morgan *et al.* 2004; Ellsworth *et al.* 2012). For the Rubisco-limited model (Eqns 2 and 5), the two unknowns are  $V_{c,\max}$  and  $R_d$ ; these can be solved using a best-fit of the data. An alternative approach is to plot  $A$  as a linear function of  $[\text{CO}_2]$  to solve for  $V_{c,\max}$  and  $R_d$  as the slope and intercept (Long & Bernacchi 2003), respectively, as

$$A = f' \cdot V_{c,\max} - R_d, \quad (15)$$

$f'$  is obtained from Eqns 2 and 5 and expressed as

$$f' = \frac{C_i - \Gamma^*}{C_i + K_c(1 + O_i/K_o)}. \quad (16)$$

As mentioned earlier,  $V_{c,\max}$  reports the apparent activity of Rubisco *in vivo*, which will vary based on Rubisco content and activation state. Even in healthy and well-illuminated leaves, under optimal conditions, Rubisco is rarely 100% activated and above a species-dependent temperature threshold a loss of activation may occur due to high temperature effects on Rubisco activase (Feller, Crafts-Brandner & Salvucci 1998; Salvucci *et al.* 2001; Spreitzer & Salvucci 2002; Salvucci & Crafts-Brandner 2004a,b).

Similarly,  $J_{\max}$  may be obtained by fitting  $A$  to  $C_i$  using linear regression (Long & Bernacchi 2003):

$$A = g'J - R_d, \quad (17)$$

where  $g'$  is obtained from Eqns 2 and 6 as

$$g' = \frac{C_i - \Gamma^*}{4.5C_i + 10.5\Gamma^*}. \quad (18)$$

Both  $J$  and  $R_d$  can be solved using this equation; but caution must be taken because small errors in  $A$  associated in the

RuBP regeneration-limited range may introduce large errors in  $R_d$  estimation. Therefore, assuming that  $R_d$  is constant in the light at any  $C_i$  allows for a value of  $R_d$  from Eqn 15 to be used in Eqn 17, thus reducing the number of free parameters. An alternative way to determine  $R_d$  is by the use of the combined gas-exchange and mass isotope approach at numerous light levels (Loreto, Delfine & Di Marco 1999).

A challenge to the linearization approach is that a subjective assessment is necessary to determine which data measured from the  $A$ -[CO<sub>2</sub>] curve is Rubisco versus RuBP regeneration-limited. Efforts to minimize the subjectivity include approaches that utilize objective information relating to maximizing the slope of Eqn 15. When RuBP regeneration-limited photosynthetic measurements are included the slope will be notably lower. Alternatively, chlorophyll fluorescence can be used to determine when  $A$  becomes RuBP regeneration-limited; this is indicated when increases in [CO<sub>2</sub>] yields no further increase in  $\Phi_{PSII}$  (Long & Bernacchi 2003). The increasing importance associated with deriving  $V_{c,max}$ ,  $J_{max}$  and  $R_d$  from measured  $A/C_i$  data has spawned a number of statistically rigorous techniques for model fitting that removes the subjective nature of previous work while characterizing the uncertainty for each estimated parameter (e.g. Patrick, Ogle & Tissue 2009; Su *et al.* 2009; Gu *et al.* 2010; Qian *et al.* 2012). A statistical analysis of six different techniques shows that there can exist a significant amount of variation in results of  $V_{c,max}$ ,  $J_{max}$  and  $R_d$  depending on the method employed (Miao *et al.* 2009).

### Using the model to predict photosynthetic responses to the environment

The model has been used extensively to examine the responses of  $A$  to biologically relevant conditions and in response to stress. The major applications of the model focus on CO<sub>2</sub> availability, temperature and light regimes, as well as interactions among these variables. The predictions using the model are dependent on values of  $V_{c,max}$  and  $J_{max}$  derived from measurements as described in the previous section. In this section, the discussion will focus on modelling  $A$  to changes in [CO<sub>2</sub>], temperature and PPFD. This will be followed with discussion on incorporating physiological responses of key global changes into the photosynthetic model. The three subsections focusing on  $A$  versus  $C_i$ , temperature and PPFD have interactive online demonstrations (The Demonstrations Project, <http://demonstrations.wolfram.com/>; Wolfram Research, Champaign, IL, USA). These demonstrations allow for real-time user manipulation of the conditions surrounding the leaf using a free CDF Player (<http://www.wolfram.com/cdf-player/>) and provide the user the opportunity to determine interacting effects of changing environmental conditions on  $A$ .

Modelling of  $A$  is generally conducted based on either intercellular [CO<sub>2</sub>] ( $C_i$ ) or chloroplastic [CO<sub>2</sub>] ( $C_c$ ). Because the focus of this review is carbon uptake, the role of the diffusive resistances of CO<sub>2</sub> from the atmosphere into the chloroplast is not discussed. However, various reviews on this

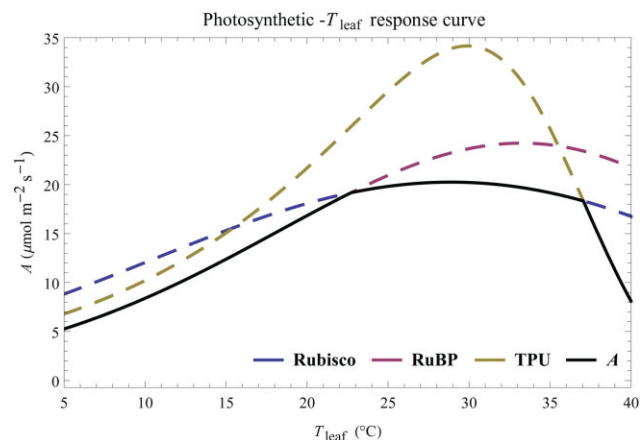
topic have been presented previously (e.g. Farquhar & Sharkey 1982; Damour *et al.* 2010). Because  $A$  is most commonly modelled using  $C_i$ , we will discuss the role of changes in  $A$  to environmental conditions on  $C_i$ ; however, neglecting the role of mesophyll conductance on fluxes of CO<sub>2</sub> for various modelling exercises can introduce error (Bernacchi *et al.* 2002; Flexas *et al.* 2012).

### Modelling A versus CO<sub>2</sub>

With instantaneous changes in [CO<sub>2</sub>] surrounding a leaf,  $A$  will generally increase with the exception of when  $A$  becomes TPU-limited. The changes in  $A$  with [CO<sub>2</sub>] are most commonly represented using an  $A$  versus  $C_i$  curve (Fig. 2; <http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToCarbonDioxide/>). Starting at the lower range of  $C_i$ , photosynthesis is generally Rubisco-limited except under conditions of very low PPFD. As  $C_i$  increases, so too does  $A$  until an inflection point is reached where  $A$  is co-limited by Rubisco and RuBP regeneration. As  $C_i$  increases beyond this first inflection,  $A$  is RuBP regeneration-limited. As  $C_i$  continues to increase, a second inflection may occur beyond which  $A$  becomes TPU-limited (Fig. 2). There are numerous factors that will influence where on the curve the inflection points will occur; these include physiological changes (e.g.  $V_{c,max}$ ,  $J_{max}$ , TPU or  $R_d$ ) and environmental changes (e.g. PPFD, temperature and/or O<sub>2</sub> concentration).

### Modelling A versus temperature

In C<sub>3</sub> species, the response of  $A$  to temperature is characterized by a steady increase to an optimum ( $T_{opt}$ ), above which  $A$  decreases at a slightly faster rate (Fig. 3; <http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToTemperature/>).

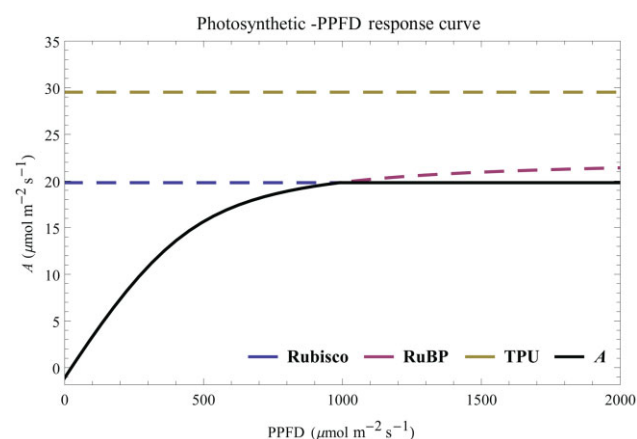


**Figure 3.** An idealized temperature response of  $A$  demonstrating the processes that limit  $A$  at each temperature. The lines, parameters and environmental conditions used to generate this figure are as in Fig. 2 with  $C_i$  set at 270  $\mu\text{mol mol}^{-1}$  over the range of temperature. This figure can be manipulated over a wide range of conditions and parameterizations at: <http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToTemperature/>

ResponsesToTemperature/). The peak of this curve may be narrow, for species specialized to extreme environments, or broad, for species in more equable climates (Sage & Kubien 2007). The shape of the temperature function is determined by the functional limitation of  $A$  at specific temperatures. The parameters underlying photosynthetic processes are highly temperature dependent, with rates for  $V_{c,max}$ ,  $J_{max}$ , TPU and  $R_d$  changing instantaneously with changes in temperature. Thus, the process that is most limiting will vary based on a number of factors. The  $T_{opt}$  is also a function of the values of  $V_{c,max}$ ,  $J_{max}$  and/or TPU. Slight changes in either  $V_{c,max}$  or  $J_{max}$  in response to changes in the environment surrounding the plant can have a strong influence on  $T_{opt}$ . Similar analysis associated with changes in the underlying physiology can be simulated using the Mathematica Demonstration link in Fig. 3.

### Modelling A versus PPFD

The response of  $A$  to PPFD is generally characterized by a quadratic equation similar to Eqn 8 (Fig. 4), although Eqn 8 represents the response of  $J$  to PPFD. Despite the similar function used to describe both  $J$  and  $A$  responses to PPFD, mechanistic modelling of  $A$  to PPFD should not exploit Eqn 8, but instead rely on the leaf  $A$  model, as the quadratic equation does not distinguish among the processes that are limiting  $A$  at high PPFD. At lower PPFD,  $A$  is RuBP regeneration-limited resulting from low rates of electron transport. The slope of the initial portion of the  $A$ /PPFD curve is commonly referred to as the quantum efficiency of  $CO_2$  assimilation and will vary based on a wide range of factors. These are incorporated into the leaf  $A$  model by changes in  $\alpha$ ,  $\beta$  and  $\Phi_{PSII}$  in Eqn 8. Often an inflection in a measured  $A$ /PPFD curve is observed at a very low PPFD attributed to changes in  $R_d$  between dark and light



**Figure 4.** An idealized curve showing the response of  $A$  to photosynthetic photon flux density (PPFD) demonstrating the processes that limit  $A$  at each PPFD. The lines, parameters and environmental conditions used to generate this figure are as in Fig. 2 with  $C_i$  set at  $270 \mu\text{mol mol}^{-1}$  over the range of PPFD. This figure can be manipulated over a wide range of conditions and parameterizations at: <http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToLight/>

(Kok 1948; Krömer 1995). Given the simplified manner in which  $R_d$  is incorporated, this inflection is not included in the model. With increasing light, the rapid increase in  $A$  with PPFD begins to diminish; the rate in which this occurs depends on the unitless curvature term  $\Theta$ . At saturating light,  $A$  can be limited by any of the three limiting processes depending on the physiology of PS and environmental conditions. Because of the uncertainty associated with whether Rubisco, RuBP regeneration or TPU limits photosynthesis under saturating light, the use of an  $A$ /PPFD response curve is not able to elucidate  $J_{max}$ . The influence of varying  $V_{c,max}$  and  $J_{max}$  on the  $A$ /PPFD curve can be simulated using the linked demonstration (<http://demonstrations.wolfram.com/ModelingPhotosyntheticResponsesToLight/>).

All the preceding examples illustrate the strong sensitivity of photosynthetic parameters to environmental variation. Moreover, specifying parameters taken from plants acclimated to appropriate environmental conditions is critical for accurately modelling the response of  $A$  to environmental changes. Small errors in model parameter estimates will propagate through the modelling steps, which can result in large errors in modelled  $A$ . For instance, significant temperature gradients exist vertically within forests such that improperly parameterized ecosystem models could overestimate carbon assimilation by up to 25% in some forest canopies, which can result in a profound effect on modelled  $A$  (Bauerle, Bowden & Wang 2007). Furthermore, the use of inappropriate photosynthetic parameters (i.e.  $V_{c,max}$ ,  $J_{max}$  and  $R_d$ ), as well as their temperature sensitivities (e.g. using a single temperature function for all species/functional groups), can lead to significant errors in the modelling of plant competition, demography, species migration and carbon fluxes within terrestrial ecosystem models (e.g. Medvigy & Moorcroft 2012), which is an important consideration for understanding ecosystem responses to global change.

### Incorporating physiological responses of key global changes into the photosynthetic model

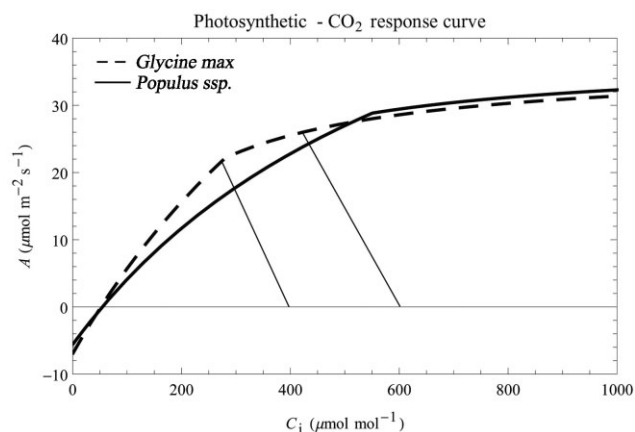
The mechanistic nature of the leaf  $A$  model also provides the opportunity to incorporate the acclimation and/or damage responses of major global change factors on  $A$ . Some key examples include the incorporation of the impacts of drought, increasing temperature,  $[CO_2]$  and ozone concentration ( $[O_3]$ ), which are all projected to play a significant role in future projections of global climate and carbon cycling (Volz & Kley 1988; Fowler *et al.* 1999; Chaves *et al.* 2002; Fuhrer 2003; Nemani *et al.* 2003; Meehl *et al.* 2007; Sitch *et al.* 2007; Fowler 2008; Van Dingenen *et al.* 2009; Ainsworth *et al.* 2012; Lei, Wuebbles & Liang 2012). Plant responses to and interactions among these factors (Leakey *et al.* 2009, 2012) span a wide range of scales and processes that influence carbon assimilation. The leaf  $A$  model provides an excellent tool for determining the consequences of these global change factors on the underlying physiology of  $A$ , expressed primarily as shifts in  $V_{c,max}$  and  $J_{max}$ .



Drought can impose both stomatal (i.e. diffusive) and non-stomatal (i.e. biochemical/metabolic and mesophyll) limitations on  $A$  which can occur simultaneously (Farquhar & Sharkey 1982; Jones 1985, 1998) and the dominant limitation can vary across a range of time scales within an ecosystem (Wilson, Baldocchi & Hanson 2000a; Grassi & Magnani 2005; Harper *et al.* 2010). Metabolic limitations are attributed, in part, to reductions in transpiration, nutrient uptake and consequently leaf nitrogen which has been shown to be correlated with  $V_{c,max}$  and  $J_{max}$  (Evans 1989; Panek & Goldstein 1999; von Caemmerer 2000; Xu & Baldocchi 2003; Panek 2004). The leaf  $A$  model has been used to estimate non-stomatal limitations through  $A/C_i$  curves to parse diffusive versus metabolic impacts of drought on  $A$  (see Flexas *et al.* 2004).

The biochemical processes underlying  $V_{c,max}$  and  $J_{max}$  acclimate to long-term (days to weeks) growth at elevated temperature and the acclimatory response differs seasonally (Onoda, Hikosaka & Hirose 2005), phenologically (Ge *et al.* 2012), and between genotypes and species (Bunce 2000; Medlyn *et al.* 2002; Yamori, Noguchi & Terashima 2005; Kattge & Knorr 2007; Weston & Bauerle 2007; Way & Sage 2008). When the growth temperature is near  $T_{opt}$ , little effect is seen in the response of  $V_{c,max}$  to slight increases in temperature (e.g. Sage *et al.* 1995); however, acclimation to moderately elevated daytime temperatures (from +3.5 to +6 °C) has been shown to decrease in  $V_{c,max}$  to differing extents for a number of species (Yamori *et al.* 2005; Weston & Bauerle 2007; Alonso *et al.* 2008; Way & Sage 2008). There are fewer data on the acclimation of  $J_{max}$  to modest increases in temperature. On average,  $J_{max}$  tends to decrease more than  $V_{c,max}$  at higher growth temperature (Bernacchi *et al.* 2003a; Way & Sage 2008; Ghannoum *et al.* 2010).

There is overwhelming evidence demonstrating significantly higher  $A$  for  $C_3$  plants grown in elevated  $[CO_2]$  (e.g. Curtis & Wang 1998; Bernacchi *et al.* 2003b; Karnosky *et al.* 2003; Nowak, Ellsworth & Smith 2004; Ainsworth & Long 2005; Ainsworth & Rogers 2007; Leakey *et al.* 2009). However, the stimulation of  $A$  is often less than predicted (Bernacchi *et al.* 2005, 2006), which is generally attributed to the down-regulation of either  $V_{c,max}$  or  $J_{max}$  (Long *et al.* 2006). In some species where the operating point of  $A$  under current atmospheric  $[CO_2]$  is near the inflection between Rubisco- and RuBP regeneration-limited  $A$ , any increase in  $[CO_2]$  is likely to lead to lower stimulation in  $A$ . These species can experience a loss in  $V_{c,max}$  due to growth in elevated  $[CO_2]$  without any consequent decrease in light saturated  $A$  (Fig. 5; Bernacchi *et al.* 2005). In other species where the operating point  $A$  is generally located well below the inflection point between Rubisco- and RuBP regeneration-limitation, increases in  $C_i$  will lead to significant increases in  $A$  (Bernacchi *et al.* 2003b; Fig. 5). Because of the inconsistency among  $C_3$  species associated with the  $C_i$  in which  $A$  operates relative to the Rubisco-RuBP regeneration inflection point, down-regulation of  $V_{c,max}$  will have a variable response on  $A$ . Rising  $[CO_2]$  is generally accepted to lead to more RuBP regeneration limitation of  $A$ , any influence of elevated  $[CO_2]$  on  $J_{max}$  is likely to lead to direct consequences on  $A$ .



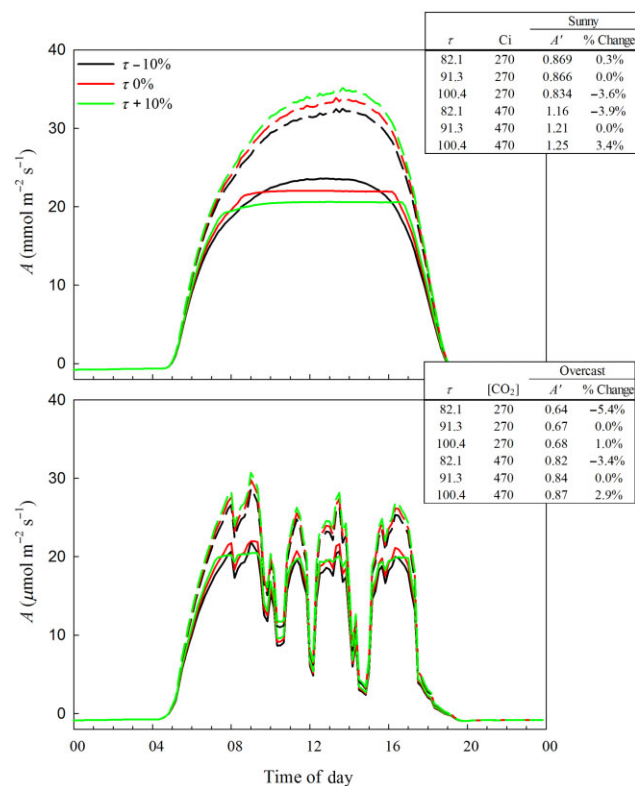
**Figure 5.** Representative  $A/C_i$  response curves modelled using  $V_{c,max}$  and  $J_{max}$  from soybean (dashed line; from Bernacchi *et al.* 2005) and poplar (solid line; from Bernacchi *et al.* 2003b). The lines intersecting  $C_i$  at 400 and 600  $\mu\text{mol mol}^{-1}$  represent the supply line of  $CO_2$  to the intercellular air spaces; where they intercept the  $x$ -axis represents atmospheric  $CO_2$  ( $C_a$ ) and where they intersect with the  $A/C_i$  function represents the operating  $C_i$  for  $A$  and the slope of the supply line is determined by the stomatal conductance of  $CO_2$  into the leaf. Soybean is stimulated less by an increase in  $C_a$  to 600  $\mu\text{mol mol}^{-1}$  as RuBP regeneration-limited  $A$  occurs relatively close to the photosynthetic operating point. The poplar, however, is Rubisco-limited even in elevated  $CO_2$ , thus a greater  $CO_2$ -induced stimulation in  $A$  occurs.

Despite the wide range of biological processes affected by  $O_3$  (Farage *et al.* 1991), the response of  $A$ ,  $g_s$  and many of the underlying biochemical reactions has been shown to decrease linearly with rising  $[O_3]$  (Mills *et al.* 2000; Ashmore 2002; Betzelberger *et al.* 2010, 2012; Lombardozzi *et al.* 2012). The primary and most sensitive biochemical response to  $O_3$  is damage to Rubisco; however, damage to photosynthetic machinery responsible for the regeneration of RuBP has been shown to occur depending on mean  $[O_3]$ , cumulative  $O_3$  exposure and developmental stage (Long & Naidu 2002; Morgan *et al.* 2004; Fiscus, Booker & Burkey 2005; Goumenaki *et al.* 2010). The impacts of this damage have been incorporated into the leaf  $A$  model by a coefficient that reflects a species' sensitivity to  $O_3$ . The coefficient accounts for a decrease in  $V_{c,max}$  and  $J_{max}$  that is linearly related to a given  $O_3$  dose (Martin *et al.* 2000, 2001).

### Identifying opportunities to improve photosynthetic rates

With increasing pressure on agriculture comes the need for a new 'Green Revolution' (von Caemmerer & Evans 2010). A potential route to increasing productivity is through increasing  $A$  for major food crops. The notion that increased  $A$  leads directly to increased biomass and yield, however, is not certain. Arguments that both support and refute the link between  $A$  and yield have been outlined previously (e.g. Long *et al.* 2006). Despite these uncertainties, the evidence suggesting higher  $A$  can yield increases in food production dictates that research should pursue these opportunities.

The leaf  $A$  model provides an excellent test-bed for various improvement scenarios. The basis for Rubisco-limited  $A$  is highly mechanistic; thus, the model confers the opportunity to assess the impacts of altering Rubisco over a range of environmental conditions. One such opportunity is altering Rubisco specificity for  $\text{CO}_2$  relative to  $\text{O}_2$  ( $\tau$ ). Previous modelling work demonstrates that  $A$  does not necessarily increase with higher  $\tau$  because a consequence of higher  $\tau$  is lower Rubisco catalytic rate ( $K_{\text{cat}}$ ,  $\text{s}^{-1}$ ; Zhu, Portis & Long 2004). Therefore, changes in  $\tau$  coincide with modelled adjustments in  $V_{\text{c,max}}$  to account for the inverse relationship with  $K_{\text{cat}}$  (Zhu *et al.* 2004). Integrating changes in  $\tau$ , driven by equal changes in  $K_c$  and  $K_o$  and altering  $V_{\text{c,max}}$  to the same extent that  $K_{\text{cat}}$  changes with  $\tau$  (Zhu *et al.* 2004), yields variable responses of  $A$  modelled over the diurnal time course depending on sunny versus overcast and current versus future elevated  $[\text{CO}_2]$  (Fig. 6). With a standard parameterization, daily integrated photosynthetic rate ( $A'$ ) for current atmospheric conditions was modelled at  $0.866 \text{ mol m}^{-2} \text{ d}^{-1}$  for



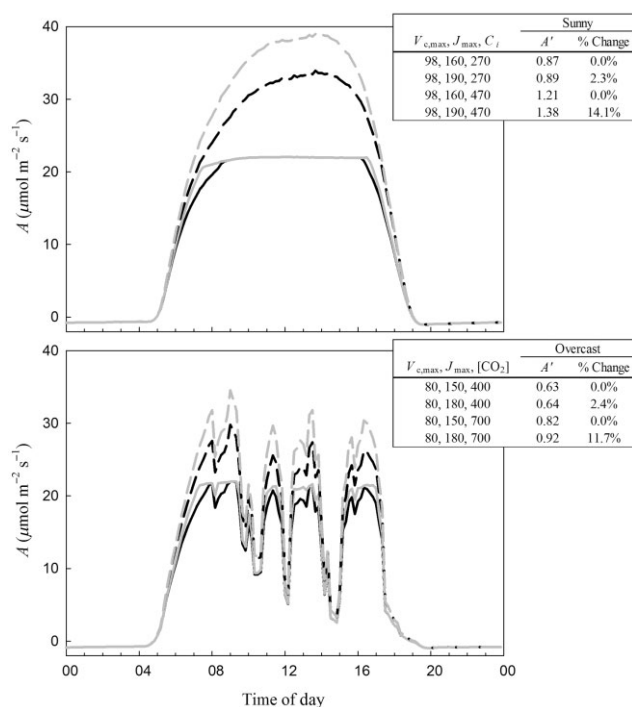
**Figure 6.** Modelled diurnal rates of net carbon assimilation ( $A$ ) simulating Rubisco with an increased  $\tau$  (+10%) and a decreased  $\tau$  (-10%). The solid lines are simulated at a  $C_i$  of  $270 \mu\text{mol mol}^{-1}$  and the dashed lines represent an increase in  $C_i$  to  $470 \mu\text{mol mol}^{-1}$ . The inset tables show the percent change in  $\tau$ , modelled daily integrated leaf-level carbon assimilation ( $A'$ ;  $\text{mol m}^{-2} \text{ d}^{-1}$ ) and the percent change in  $A'$  within a  $[\text{CO}_2]$  relative to no change in  $\tau$ . Meteorological conditions for the Sunny (top panel) and overcast (bottom panel) days are shown in Fig. 1. This figure can be manipulated over a wide range of conditions and parameterizations at: <http://demonstrations.wolfram.com/ModelingDiurnalPhotosynthesis/>

the sunny day and  $0.673 \text{ mol m}^{-2} \text{ d}^{-1}$  for the overcast day (Fig. 6). Increasing  $\tau$  by 10% yields a -4% decrease in  $A'$  for the sunny day and a 1% increase for the overcast day, whereas decreasing  $\tau$  by 10% yields no change for the sunny day and a 5.5% decrease in  $A'$  for the overcast day (Fig. 6). These predictions are based on the differential effect of  $\tau$  on Rubisco compared with RuBP regeneration-limited  $A$ . When  $A$  is RuBP regeneration-limited, an increase in  $\tau$  will lead to higher  $A$  because of a suppression in photorespiration, whereas when  $A$  is Rubisco-limited, the suppression of photorespiration is linked with a lower catalytic rate, thus driving a decrease in  $A$  (Zhu *et al.* 2004). In elevated  $[\text{CO}_2]$ ,  $A$  is more likely to be RuBP regeneration-limited over most of the day; thus, suppressing photorespiration through an increase in  $\tau$  will almost always lead to higher  $A$  (Fig. 6). Therefore, the opportunities for improving the kinetics of Rubisco under current atmospheric conditions may not extend to future atmospheric conditions.

Because  $A$  is light-limited for at least a portion of the day for upper canopy leaves and over a significant portion of the day for shaded leaves, and in addition is likely to become more RuBP regeneration-limited at future  $[\text{CO}_2]$  (Sage, Sharkey & Seemann 1988, 1989; Woodrow & Berry 1988; Long & Drake 1991; Sage 1994; Woodrow 1994), increasing rates of RuBP regeneration are likely to have a more meaningful and lasting impact on productivity (Fig. 7). While RuBP regeneration-limited  $A$  is traditionally assumed to represent limited light availability for electron transport, recent research demonstrates that at least a co-limitation by key PCR cycle enzymes exist (Harrison *et al.* 2001; Raines 2003; Lefebvre *et al.* 2005). Using the leaf  $A$  model to predict the benefits of a higher rate of RuBP regeneration by increasing  $J_{\text{max}}$  shows that under current atmospheric conditions, when  $A$  is light-limited a higher  $J_{\text{max}}$  confers higher  $A$  although no increase occurs when  $A$  is Rubisco-limited. For a simulated leaf at the top of the canopy on a sunny day, the increase in  $J_{\text{max}}$  only increases  $A$  when PPFD is not saturating, namely in the morning and evening (Fig. 7). However, in future  $[\text{CO}_2]$ , the advantage of a higher  $J_{\text{max}}$  becomes increasingly evident (Rosenthal *et al.* 2011). Any increase in  $J_{\text{max}}$  has an effect of increased  $A$  up to the point when  $A$  becomes Rubisco-limited (Fig. 7).

### Scaling from the leaf

The role of the leaf  $A$  model in understanding the underlying mechanisms associated with steady-state PS provides a unique opportunity to scale photosynthesis beyond the leaf at various temporal and spatial scales. When assessing ecosystem productivity, there exists a variety of methods in which the net uptake of  $\text{CO}_2$  can be measured or indirectly inferred, including canopy chambers (Leadley & Drake 1993; Steduto *et al.* 2002), eddy covariance (Baldocchi 2003), remote sensing techniques (Field, Randerson & Malmstrom 1995; Prince & Goward 1995; Running *et al.* 2004; Fuentes *et al.* 2006; Gitelson *et al.* 2006; Ryu *et al.* 2011; Serbin *et al.* 2012) or through combinations of various techniques (e.g. Xiao *et al.* 2011). However, the processes that drive the net



**Figure 7.** Modelled diurnal photosynthetic rates simulating increases in  $J_{max}$  from 160 to 190  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The solid lines are simulated at a  $C_i$  of 270  $\mu\text{mol mol}^{-1}$  and the dashed lines represent an increase in  $C_i$  to 470  $\mu\text{mol mol}^{-1}$ . The inset tables show the change in  $J_{max}$ ,  $A'$  ( $\text{mol m}^{-2} \text{d}^{-1}$ ) and % change in  $A'$ . Meteorological conditions for the Sunny (top panel) and overcast (bottom panel) days are shown in Fig. 1. This figure can be manipulated over a wide range of conditions and parameterizations at: <http://demonstrations.wolfram.com/ModelingDiurnalPhotosynthesis/>

$\text{CO}_2$  flux for vegetation becomes more complex with larger spatial scales. In addition to the processes behind the leaf fluxes (PS, PR and  $R_d$ ) are the ecosystem fluxes of  $\text{CO}_2$  by vegetation (non-leaf organs) and heterotrophs (e.g. soil microbial communities). Because the methods to assess net ecosystem carbon fluxes are a conglomeration of different processes, the leaf  $A$  model is one tool that can help tease apart the gross primary production (ecosystem-scale  $A$ ) from autotrophic and heterotrophic respiration (reviewed in Reichstein *et al.* 2005).

Various canopy  $A$  models have been developed that rely on the fundamental leaf  $A$  model (e.g. Monteith 1981; Sellers *et al.* 1992; Amthor 1994; Sands 1995; dePury & Farquhar 1997; Wang & Leuning 1998; Chen *et al.* 1999). Recent advances in the understanding of the parameters required for modelling  $A$ , increasing numbers of datasets employing a range of measurement techniques, and increasingly more accessible computational power are leading the development and application of higher detail multilayer canopy and ecosystem-scale models (e.g. Reynolds *et al.* 1992; Medvigy *et al.* 2009; Drewry *et al.* 2010a; Kobayashi *et al.* 2012). However, regardless of the advances made in various components of ecosystem modelling, the leaf  $A$  model

(Farquhar *et al.* 1980), with improved temperature functions (Bernacchi *et al.* 2001, 2002, 2003a), has remained an integral component of modelling ecosystem-scale carbon, energy and moisture fluxes.

One indication of the influence that the leaf  $A$  model has had on ecosystem modelling is the importance of aforementioned photosynthetic parameters such as  $V_{c,max}$  in reproducing gross primary productivity (GPP) for ecosystem-scale observations. In practice, terrestrial biosphere models (TBMs) that provide a mechanistic understanding of carbon cycling use a combination of leaf-level and eddy covariance measurements from single site or groups of eddy covariance towers to infer key photosynthetic parameters such as  $V_{c,max}$ . Then, the parameters are subsequently lumped into broadly defined PFTs. These models do not provide perfect representations of natural systems or the underlying controls on  $\text{CO}_2$  exchange, and as such, key photosynthetic parameters such as  $V_{c,max}$  can be highly variable within individual PFTs (Kattge *et al.* 2009; Bonan *et al.* 2011; Groenendijk *et al.* 2011). Partially as a response to this variation of photosynthetic parameters within PFTs, representations of the natural environment and structural errors (i.e. imperfect mathematical simplifications of ecological phenomenon) can be offset by adjusting parameters, such as  $V_{c,max}$ , in order to produce modelled  $A$  or GPP that agrees with canopy or ecosystem-scale observations (Chen *et al.* 2011; Bonan *et al.* 2012). Despite the challenges of different model structures and parameterizations, new techniques utilizing model-data assimilation provide an efficient means to integrate observations of important photosynthetic parameters in TBMs (LeBauer *et al.* 2012; Wang, LeBauer & Dietze 2013). These approaches address issues of observation variability, uncertainty and scale, as well as the uncertainties associated with model structure and fluxes (e.g. GPP), in a much more robust fashion than simple tuning of model parameters (e.g. Bonan *et al.* 2012) and allow for the comparison of model parameterizations across sites and TBMs.

## REMOTE SENSING APPLICATIONS AND PHOTOSYNTHESIS MODELLING

The ability to monitor photosynthetic status with remotely sensed data is based on the principle that plant physiological properties, fundamentally tied to the biochemical composition, structure and distribution of foliage within plant canopies, are reflected in the optical characteristics of the canopy that can be observed using remote-sensing instruments (Curran 1989; Kokaly *et al.* 2009; Ollinger 2011). As such, a considerable amount of remote-sensing research has focused on the development of methods utilizing the shortwave (i.e. 300–3000 nm) infrared wavelengths for the indirect characterization of photosynthetic functioning of vegetation (e.g. Sellers *et al.* 1992; Field *et al.* 1995; Gamon, Serrano & Surfus 1997; Grace *et al.* 2007; Coops *et al.* 2010; Damm *et al.* 2010; Frankenberg *et al.* 2011). Furthermore, research has focused on the detection of the biochemical, structural and physiological characteristics of leaves and plant canopies that govern photosynthetic carbon uptake (e.g. Wessman *et al.*

1988; Martin & Aber 1997; Kokaly *et al.* 2009; Middleton *et al.* 2009; Asner *et al.* 2011).

Along with these approaches, efforts have explored the ability to relate variations in spectral optical properties to the key parameters of the leaf  $A$  model,  $V_{c,max}$  and  $J_{max}$  (Stylinski *et al.* 2000; Wang, Iio & Kakubari 2008; Doughty, Asner & Martin 2011; Dillen *et al.* 2012; Serbin *et al.* 2012). In particular, Doughty *et al.* (2011) and Serbin *et al.* (2012) illustrated that the use of reflectance contributions from the visible (400–700 nm), near-infrared (700–1300 nm) and shortwave infrared (1300–2500 nm) rather than narrowband indices offers considerable potential for the detection of photosynthetic metabolism, as well as the ability to detect short-term (instantaneous), dynamic variations in  $V_{c,max}$  and  $J_{max}$  related to changes in environmental conditions (e.g. temperature; Serbin *et al.* 2012). This presents a critical step towards the rapid and continuous monitoring of plant physiological parameters relevant for global change research, as well as for improving TEM parameterizations over broad regions. An important consideration of these optical techniques is the need to characterize the spatial variation in surface temperatures (i.e. leaf and canopy) at the time of observation in order to normalize remotely sensed values of  $V_{c,max}$  and  $J_{max}$  to a reference temperature (e.g. Bernacchi *et al.* 2001, 2002, 2003a). This combined optical and thermal approach enables the direct integration of remotely sensed variations in  $V_{c,max}$  and  $J_{max}$  into leaf- and canopy-scale photosynthesis models or TBMs.

The ability to map and monitor changes in photosynthetic biochemistry using remote-sensing techniques (Kokaly *et al.* 2009; Ustin *et al.* 2009; Asner *et al.* 2011) illustrates the importance of linking the leaf  $A$  model with measurements over large spatial scales. At the leaf level, the combined use of traditional gas-exchange measurements with observations of leaf optical properties has yielded considerable insight into the functioning of vegetation (e.g. Peñuelas, Filella & Gamon 1995; Gamon *et al.* 1997; Stylinski *et al.* 2000; Guo & Trotter 2004; Serbin *et al.* 2012). While scaling up the relationships between spectral reflectance, biochemistry and PS remains challenging (Nichol *et al.* 2002; Grace *et al.* 2007; Hilker *et al.* 2008; Coops *et al.* 2010; Asner *et al.* 2011), this is a critical area of research as remote-sensing observations offer the only true, synoptic opportunity to continuously monitor terrestrial  $A$  at a regional or global scale. This is particularly important given the uncertainty of global change on terrestrial ecosystems.

## CONCLUSION

A number of methods exist for measuring or inferring  $A$  over a wide range of scales, including leaf gas exchange (Long & Bernacchi 2003), canopy chamber methods (Leadley & Drake 1993; Johnson, Polley & Whitis 2000), eddy covariance (Baldocchi 2003) and remote sensing techniques (Field *et al.* 1995; Damm *et al.* 2010; Frankenberg *et al.* 2011; Serbin *et al.* 2012). The basis for the ability to compare  $A$  among these spatial scales is through modelling. The leaf  $A$  model (Farquhar *et al.* 1980) provides the foundation for scaling  $A$

among a variety of spatial and temporal ranges while also providing the basis for generating predictions and hypotheses. A key attribute of the leaf  $A$  model is the mechanistic basis upon which equations are derived. In the context of scaling  $A$  to the globe, the leaf  $A$  model provides the backbone for predictions of GPP that are being validated against an increasing number of remote sensing techniques. Recent advances in remote-sensing methods to acquire the parameters needed to model  $A$  ( $V_{c,max}$  and  $J_{max}$ ; e.g. Serbin *et al.* 2012) will further help to constrain models using the most accurate parameterizations.

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