Viewpoints

A roadmap for improving the representation of photosynthesis in Earth system models

Summary

Accurate representation of photosynthesis in terrestrial biosphere models (TBMs) is essential for robust projections of global change. However, current representations vary markedly between TBMs, contributing uncertainty to projections of global carbon fluxes. Here we compared the representation of photosynthesis in seven TBMs by examining leaf and canopy level responses of photosynthetic CO_2 assimilation (A) to key environmental variables: light, temperature, CO_2 concentration, vapor pressure deficit and soil water content. We identified research areas where limited process knowledge prevents inclusion of physiological phenomena in current TBMs and research areas where data are urgently needed for model parameterization or evaluation. We provide a roadmap for new science needed to improve the representation of photosynthesis in the next generation of terrestrial biosphere and Earth system models.

Introduction

Fossil energy use is the dominant driver of the increase in atmospheric CO_2 concentration (C_a) and the principal cause of global climate change Intergovernmental Panel on Climate Change (2013). Many of the observed and projected impacts of rising C_a portend increasing environmental and economic risk, yet the uncertainty surrounding the projection of our future climate by Earth system models (ESMs) is unacceptably high (Friedlingstein *et al.*, 2006, 2014).

Although CO_2 emissions associated with anthropogenic activity are notable (11 Pg C yr^{-1}), they represent < 10% of the gross carbon fluxes between the land surface and the atmosphere (Beer *et al.*, 2010; Boden *et al.*, 2013; Le Quéré *et al.*, 2015). Terrestrial photosynthetic CO_2 assimilation (A) is the largest of these CO_2 fluxes (~120 Pg C yr^{-1}), subsidizing our use of fossil fuels through the net assimilation of about one-third of the CO_2 emissions associated with anthropogenic activities (Le Quéré *et al.*, 2015). However, there is critical uncertainty about how the terrestrial carbon sink will be affected by changes in A with rising C_a, temperature and drought (Gregory *et al.*, 2009; IPCC, 2013; Friedlingstein *et al.*, 2014). Therefore, reducing the uncertainty associated with model representation of A is an essential part of improving confidence in projections of global change (Ciais *et al.*, 2013).

In this study we have focused on photosynthesis, but recognize that improving the understanding and projection of the terrestrial biosphere's response to global change also depends on realistically representing many additional processes that are down stream of carbon assimilation (e.g. carbon allocation, plant and soil respiration, and nutrient cycling). Of particularly relevance to photosynthesis is the allocation of extra carbon to leaf area in trees grown at elevated C_a (Ainsworth & Long, 2005). Model representation and integration of these processes, and how the balance between them shifts in their individual and combined responses to environmental drivers, will also be critical in order to capture whole system responses, but such a comprehensive discussion is beyond the scope of this study.

We examined model representations of A in seven terrestrial biosphere models (TBMs). These models include four that represent the land component of ESMs which were part of the recent Coupled Model Intercomparison Project (CMIP5) – the main resource for the IPCC Fifth Assessment Report (IPCC, 2013; Friedlingstein *et al.*, 2014). Our approach focuses on how physiological responses are represented by TBMs. We compared modeled responses of A to key environmental variables in order to identify areas of model divergence that reflect gaps in current understanding of the physiological and environmental controls of A. In the second half of the paper, we turn to issues of scale – vertical, horizontal and temporal – and consider how representation and parameterization of leaf-level processes is scaled to the canopy within current model frameworks.

We had three goals: (1) understand how models differ in their representation of A; (2) identify gaps in current understanding of A that contribute to uncertainty in model output; (3) identify areas where current process knowledge and emerging data sets can be used to improve model skill. This study provides recommendations for immediate improvements that can be made to current model representation of A and also highlights the scientific activity needed to further advance representation of A in the next generation of TBMs.

Representation of leaf photosynthesis in terrestrial biosphere models

Current model structure and parameterization

The Farquhar, von Caemmerer and Berry (FvCB) model of A (Farquhar *et al.*, 1980; von Caemmerer & Farquhar, 1981; von Caemmerer, 2000) provides a robust mechanistic representation of A in C_3 species, and is the foundation for model estimation of gross

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primary production (GPP) in many TBMs (Cramer *et al.*, 2001; Rogers, 2014), including the seven models considered here (BETHY, CLM, ED2, G'DAY, JSBACH, JULES and O-CN; Table 1). The formulations of the FvCB model used in these TBMs include elements of; Collatz *et al.* (1991), in CLM, ED2 and JULES; Foley *et al.* (1996), in ED2; and Kull & Kruijt (1998), in O-CN (Table 1). The FvCB model represents photosynthetic CO_2 assimilation as the most limiting of two biochemical processes: Rubisco carboxylation, and ribulose-1,5-bisphosphate (RuBP) regeneration driven by electron transport. These processes limit A in most environments; however, Sharkey (1985) subsequently described how limitations on triose phosphate utilization (TPU limitation) could also limit A under some conditions. Only two models in this study included TPU limitation (CLM and JULES; Table 1).

Similar biochemical models have been developed for the C_4 photosynthetic pathway (von Caemmerer, 2000). For reasons of space, we limit our discussion to model treatment of C_3 photosynthesis. However we note that a similar exercise focused on C_4 photosynthesis would be valuable.

Models typically represent stomatal conductance (g_s) using a coupled relationship with A that varies with atmospheric, or leaf-surface, CO_2 concentration, and some measure of atmospheric humidity. This model approach was originally formulated by Ball *et al.* (1987), who used a direct dependence on relative humidity (RH) in their equation for g_s. Ball *et al.*'s (1987) equation is still widely used in many TBMs, including CLM. Leuning (1995) suggested an alternative equation that depends on vapor pressure deficit (VPD) rather than RH. ED2 uses the Leuning (1995) equation, while JULES uses a very similar equation developed by Jacobs (1994). The approaches to represent g_s implemented by the models considered here are quite diverse (Table 1) which has a wide-ranging impact on the model outputs we considered.

The TBMs in this study represent vegetation using broad plant functional types (PFTs). The FvCB model is parameterized with a number of important constants that are typically the same for all PFTs. PFTs are distinguished with respect to photosynthesis through differences in the estimates of the maximum carboxylation rate of Rubisco ($V_{c,max}$), the maximum rate of electron transport (J_{max}) and the slope of the stomatal conductance response. Several groups are now working towards next-generation vegetation models in which PFTs are replaced by 'trait-based approaches' (Wullschleger *et al.*, 2014). This catchall phrase includes leveraging trait-environment linkages (van Bodegom *et al.*, 2014; Reich, 2014; Ali *et al.*, 2015), optimality approaches (Xu *et al.*, 2012; Meir *et al.*, 2015), trait filtering (Fisher *et al.*, 2012) and adaptive global vegetation models (Scheiter *et al.*, 2013). However, our review is relevant to these approaches as well, as they still employ similar representations of photosynthesis. The key difference lies in parameterization, which we discuss when considering scaling to landscapes.

Mesophyll conductance

In C_3 species, mesophyll conductance (g_m) describes the conductance to CO_2 diffusion from the intercellular airspace within a leaf to the sites of carboxylation within chloroplasts (von Caemmerer & Evans, 1991; Flexas *et al.*, 2012). It is one of the four main physiological processes limiting CO_2 uptake and fixation, the others being g_s and the biochemical activity of Rubisco and RuBP regeneration. To our knowledge, there are no land models that currently contribute to the IPCC assessments that consider g_m. This absence reflects the challenge of adding further complexity to the models, but also the uncertainty and technical difficulty of the measurements required to estimate g_m.

Response curves of A to intercellular [CO_2] (C_i) are routinely used to infer the maximum biochemical activity of Rubisco and RuBP regeneration, i.e. $V_{c,max}$ and J_{max}. When the FvCB model was conceived, the assumption was made that the difference between C_i and the [CO_2] within the chloroplast (C_c) was sufficiently small that it could be ignored. Subsequently, improved measurement techniques for g_m have shown that it can impose a significant limitation on A which varies with temperature, and there are significant species differences in these responses (von Caemmerer & Evans, 2015). If g_m is not taken into account in the analysis of A-C_i curves, the true $V_{c,max}$ will be underestimated (von Caemmerer, 2000; Niinemets *et al.*, 2009; Sun *et al.*, 2014). Furthermore, temperature responses of $V_{c,max}$ and J_{max} derived from gas exchange measurements will not necessarily reflect the temperature dependence of the underlying biochemistry alone, but will also reflect the temperature response of g_m (Medlyn *et al.*, 2002a). The use of apparent parameters is problematic if modelers wish to incorporate new data on the underlying biochemistry of photosynthesis. For example, a recent biochemical survey of the catalytic diversity in Rubisco revealed significant and marked variation in key parameters across 75 species (Orr *et al.*, 2016). These data cannot be used directly in models without including g_m in model structures, highlighting the need for improved understanding and model representation of g_m.

Several TBMs currently use linear relationships between apparent $V_{c,max}$ (obtained from A-C_i curves) and leaf nitrogen to derive $V_{c,max}$ prognostically. If g_m were to be incorporated into future TBMs, new algorithms linking $V_{c,max}$ to leaf N content would be required as the $V_{c,max}$ used in the relationship would need to be derived as a function of C_c not C_i. Currently a reliance on apparent V_{cmax}–leaf N relationships means that models underestimate the amount of N partitioned to Rubisco, or put another way, overestimate the nitrogen use efficiency of CO_2 carboxylation by Rubisco.

It is clear that an improved understanding of g_m remains a critical research area. Despite recent important progress that may simplify prediction of g_m (Tholen *et al.*, 2012), we feel that immediate inclusion of g_m in TBMs is premature. 'Apparent' parameters derived from A-C_i response curves, which implicitly account for g_m, have been used successfully to model A in many ecosystems at the leaf and canopy level (e.g. Bernacchi *et al.*, 2003; Medlyn *et al.*, 2005; Thum *et al.*, 2007). Until understanding and measurement of g_m matures, its inclusion in TBMs will likely drive additional uncertainty. Furthermore, the modeling community currently has access to a substantial dataset (albeit heavily biased to the mid-latitudes) of 'apparent' parameters but almost no data for $V_{c,max}$ and J_{max} derived from A-C_c curves. Including g_m now would dramatically shrink the amount of data available for model

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Table 1 Model representation of the response of C_3 photosynthesis to key environmental variables used for this study

BETHY	CLM4.5	ED2	G'DAY	JSBACH	JULES	O-CN
Leaf photosynthesis (response to C_a)						
Farquhar *et al.* (1980), no TPU limitation	Farquhar *et al.* (1980), includes TPU limitation and co-limitation from Collatz *et al.* (1991)	Collatz *et al.* (1991) and Foley *et al.* (1996); no TPU limitation	Farquhar *et al.* (1980), no TPU limitation	Farquhar *et al.* (1980), no TPU limitation	Collatz *et al.* (1991), TPU limitation included	Farquhar type (Farquhar *et al.*, 1980) following Kull & Kruijt (1998)
Stomatal conductance (response to atmospheric VPD, C_a soil moisture and A)						
Minimum of (1) stomatal conductance necessary to realize maximum C_i : C_a and (2) soil water availability (Federer, 1982)	Sensitivity to atmospheric RH, C_a and A from Ball *et al.* (1987) Sensitivity to soil moisture is from a β factor applied to the intercept of the Ball *et al.* (1987) model. The β factor is summed over soil layers, weighted by root fraction in each layer and calculated based on soil moisture content	Sensitivity to atmospheric VPD, C_a and A from Leuning (1995) Water supply is proportional to soil moisture root biomass. If the open stomata demand exceeds supply then g_s is linearly scaled between open and closed stomata	Sensitivity to atmospheric VPD, C_a and A from Medlyn *et al.* (2011) Sensitivity to soil moisture from β factor applied to the slope of the stomatal response (Medlyn *et al.*, 2011). Soil moisture content is expressed as a fraction of total plant available water and dependent on soil type	Estimates potential A for any given condition assuming a maximal C_i: C_a resulting from a maximum potential g_s When soil moisture content falls below 50% of plant available water maximum potential g_s is reduced linearly	Sensitivity to atmospheric VPD, C_a and A from modification of Leuning (1995) model as proposed by Jacobs (1994)	Non-linear sensitivity to specific humidity deficit and C_i. The latter is necessary because A for g_s is evaluated at saturating C_i A β factor is applied to the slope of the stomatal response when soil moisture content falls below 50% of plant available water
Leaf photosynthesis (response to light)						
Rectangular hyperbola, with realized quantum yield and A_{sat} calculated from Farquhar model	Non-rectangular hyperbola, with realized quantum yield and A_{sat} calculated from Farquhar model	Hyperbolic function, with realized quantum yield and A_{sat} calculated from the Collatz *et al.* (1991) model, no J_{max} term included	Non-rectangular hyperbola, with realized quantum yield and A_{sat} calculated from Farquhar model	Rectangular hyperbola, with realized quantum yield and A_{sat} calculated from Farquhar model	Hyperbolic function, with realized quantum yield and A_{sat} calculated from the Collatz *et al.* (1991) model, no J_{max} term included	Explicit separation into light saturated and limited regions: A_{sat} is calculated from Farquhar *et al.* (1980). Light limited A is assumed to be proportional to light absorption (Kull & Kruijt, 1998)
Leaf photosynthesis (response to temperature)						
Temperature dependence of kinetic constants follows Bernacchi *et al.* (2001). $V_{c,max}$ and J_{max} are peaked Arrhenius functions of temperature	Temperature dependence of kinetic constants follows Bernacchi *et al.* (2001). $V_{c,max}$ and J_{max} are peaked Arrhenius functions of temperature. TPU has the same temperature response as V_{cmax}	Follows Collatz *et al.* (1991) and Foley *et al.* (1996). The temperature dependent kinetic constants follow a modified Arrhenius function. A phenomenological thermal downscaling of $V_{c,max}$ occurs at low and high temperatures (Medvigy *et al.*, 2009)	Temperature dependence of kinetic constants follows Bernacchi *et al.* (2001). $V_{c,max}$, J_{max} and R_d are peaked Arrhenius functions (Medlyn *et al.*, 2002a,b)	Temperature dependence of kinetic constants and $V_{c,max}$ follow an Arrhenius function, Γ^* and J_{max} vary linearly with temperature	Follows Collatz *et al.* (1991), the temperature dependence of kinetic constants follows a Q_{10} function. $V_{c,max}$ has a peaked temperature function calculated from $V_{c,max}$ at 25°C using vegetation-specific optimal temperature ranges	Temperature dependence of kinetic constants and $V_{c,max}$ follows Bernacchi *et al.* (2001). The temperature dependence of J_{max} is derived from June *et al.* (2004)

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Table 1 (Continued)

BETHY	CLM4.5	ED2	G'DAY	JSBACH	JULES	O-CN
Leaf photosynthesis (response to soil moisture content)						
	A β factor is applied to $V_{c,max}$. The β factor, calculated based on soil moisture potential, is summed over soil layers, weighted by root fraction in each layer.		A β factor is applied to J_{max} and $V_{c,max}$. Soil moisture content is expressed as a fraction of total plant available water and dependent on soil type		Potential *A* is multiplied by a soil water stress factor related to the mean soil moisture concentration in the root zone and the critical and wilting point soil water concentrations (Cox *et al.*, 1998)	A β factor reduces $V_{c,max}$ and J_{max} when plant available water < 20% (Friend, 2010)
Canopy scaling						
Multiple canopy layers, using Sellers's (1987) two-stream approximation. $V_{c,max}$ and J_{max} declines exponentially within the canopy following Lloyd *et al.* (2010)	The multi-layer option explicitly resolves direct and diffuse radiation for sunlit and shaded leaves at each level in the canopy. Both options use Sellers's (1987) two-stream approximation for radiative transfer. Nitrogen declines exponentially with greater cumulative LAI.	Cohort-based model with the number of layers equal to the number of cohorts. Cohorts differ by PFT definition. Radiation penetration is defined by leaf area index (LAI) and the leaf and wood single scattering albedos. There is no separation of sunlit and shaded foliage in the default version	Big-leaf model, assuming exponential light and nitrogen distributions. Daily *A* calculated using Gaussian integration (Sands, 1996)	Multiple canopy layers, using Sellers's (1987) two-stream approximation. LAI typically = 3. For LAI < 3, N (and hence $V_{c,max}$, J_{max}) is distributed evenly in the canopy (assumed to be open). For LAI > 3, N follows the distribution of light (exponential decline).	Multi-layer canopy using the two-stream approximation from Sellers (1987) solving direct and diffuse radiation for sunlit and shaded leaves at each canopy layer. Includes exponential vertical nitrogen distribution of photosynthetic capacity and leaf respiration	Multiple canopy layers with diffuse and direct radiation streams following Spitters (1986) . Nitrogen declines exponentially with greater cumulative LAI, affecting $V_{c,max}$ and J_{max}
Key model references						
Knorr & Heimann (2001)	Bonan *et al.* (2011, 2012), Oleson *et al.* (2013)	Medvigy *et al.* (2009), Moorcroft *et al.* (2001)		Knorr & Heimann (2001)	Best *et al.* (2011), Clark *et al.* (2011), Harper *et al.* (2016)	Zaehle & Friend (2010), Friend (2010)

BETHY, Biosphere Energy Transfer Hydrology scheme; CLM4.5, the Community Land Model version 4.5; G'DAY, Generic Decomposition and Yield model; JSBACH, Joint Scheme for Biosphere Atmosphere Coupling in Hamburg; JULES, Joint UK Land Environment Simulator; O-CN, an extension of the Organizing Carbon and Hydrology in Dynamic Ecosystems model that includes key N cycle processes.

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parameterization. However, it is important to note that inclusion of g_m in models is essential if carbon isotope discrimination is to be inferred (Ethier & Livingston, 2004; Suits *et al.*, 2005).

Recommendation: (1) Greater process knowledge of g_m will be required before it can be included in TBMs. Specific needs include improved understanding of variation in g_m across PFTs and how it is affected by environmental drivers such as light and temperature.

Short-term leaf level responses to environmental variables in current model structures

Our goal was to understand and compare the physiological responses inside these seven TBMs (Table 1). We focused on one particular PFT – a broad leaved deciduous tree – and defined several environmental and physiological variables which provided standard conditions for model intercomparison: instantaneous quantum flux density (Q) = 1500 μmol mol^{-1}, upper canopy sunlit leaf temperature = 25°C, C_a = 380 μmol mol^{-1}, [O_2] = 210 mmol mol^{-1}, VPD = 1 kPa, soil moisture content at field capacity and $V_{c,max}$ = 60 μmol m^{-2} s^{-1}. In the following sections we present and discuss leaf level responses to light, temperature, C_a, VPD and soil water content.

Short-term response to light

The initial slope of the photosynthetic light response curve is determined by the maximum quantum yield of CO_2 assimilation. For clarity, here we distinguish between the *intrinsic* quantum yield (Φ_{int}), which is the initial slope of the relationship between A and absorbed Q under non-photorespiratory conditions and the *realized* quantum yield (Φ_{real}), which we define as the photosynthetic rate per unit incident light at Q = 100 μmol m^{-2} s^{-1} in our standard conditions (Table 2 and the initial slope of the A–Q response in Fig. 1a). The Φ_{int} is generally an input parameter to the models (Table 2) whereas the realized quantum yield is calculated by the models using the FvCB equations, and depends not only on the Φ_{int} but also on the assumed values for the Rubisco kinetic constant Γ^* (the CO_2 compensation point in the absence of mitochondrial respiration), the low light C_i, the leaf absorptance (a), and the convexity of the light response curve (Θ). Model variation in the choice of kinetic constants, low light C_i, a and Θ are summarized in Table 2. The CLM assumes that Φ_{int} is equal to the theoretical maximum of $(1-f)/8$, where f = 0.15 and is used to correct for the spectral quality of light (von Caemmerer, 2000). As a result, CLM has the highest Φ_{real} (0.053 mol mol^{-1}; Table 2; Fig. 1a). The other models are parameterized with quantum yield inputs that result in a calculated Φ_{int} that is below the theoretical maximum and the resulting values for Φ_{real} are lower than those for CLM (Table 2). Despite a parameterization that is broadly consistent with other models, the initial slope of the A–Q response of O-CN is strikingly low and results from a limitation of A by light harvesting at low Q (Kull & Kruijt, 1998; Table 1).

Experimental studies focused on understanding natural variation in quantum yield have shown that there is little variation in Φ_{int} under unstressed conditions across a wide range of species, with an average value of 0.092 mol mol^{-1} (Long *et al.*, 1993; Singsaas *et al.*, 2001), comparable with the range of Φ_{int} used in the models considered here (0.07–0.106, Table 2). However, Φ_{int} can be substantially lower in the field, particularly in stressed conditions (Singsaas *et al.*, 2001; Niinemets *et al.*, 2004; Medlyn *et al.*, 2007;

Table 2 Parameters used by the models in this study (Table 1)

	BETHY	CLM4.5	ED2	G'DAY	JSBACH	JULES	O-CN
K_c at 25°C (μmol mol^{-1})	404.9	404.9	300	404.9	404.9	300	404.9
K_o at 25°C (mmol mol^{-1})	278.4	278.4	294	278.4	278.4	300	278.4
Γ^* at 25°C (μmol mol^{-1})	42.75	42.75	41.57	42.75	42.75	40.38	42.75
Source of kinetic constants	Bern	Bern	Foley	Bern	Bern	Collatz	Bern
JV_{ratio}	1.92	1.97	NA	2.00	1.90	NA	2.08
J_{max} (μmol m^{-2} s^{-1})	115 (86)	115 (85)	NA	120 (90)	114 (86)	NA	126 (94)
Absorbtance	0.88	0.85	0.73	0.85	0.88	0.85	0.80
Convexity	NA	0.98 & 0.95[a]	NA	0.7	NA	0.83 & 0.93[a]	NA
C_i at low light (μmol mol^{-1})	348	400	400	293	348	280	ND
Model input for quantum yield	0.28[b]	0.4250[b]	0.08[d]	0.26[c]	0.28[b]	0.08[d]	0.08[d]
Calculated ϕ_{int}	0.070	0.106	0.080	0.076	0.070	0.080	0.080
ϕ_{real}	0.049	0.053	0.038	0.038	0.050	0.045	0.022

The Michaelis–Menton constants of Rubisco for carbon dioxide (K_c) and oxygen (K_o), the CO_2 compensation point in the absence of nonphotorespiratory michondrial respiration in the light (Γ^*) and the sources of those kinetic constants (Bern, Bernacchi *et al.* (2001); Collatz, Collatz *et al.* (1991); Foley, Foley *et al.* (1996)). Where applicable the model specific ratio of the maximum electron transport rate (J_{max}) to maximum photosynthetic capacity ($V_{c,max}$), the (JV_{ratio}), was used to calculate J_{max} for standard conditions, low nitrogen conditions are shown in parentheses. Leaf absorbtance; the convexity term ([a]for the transition between Rubisco and light limited and light limited and triose phosphate utilization (TPU) limited A, respectively); the intercellular [CO_2] (C_i) at low light. Three model inputs were used to parameterize quantum yield ([b]quantum yield of electron transport based on absorbed light, [c]quantum yield of electron transport based on incident light and [d]quantum yield of photosynthesis based on absorbed light and measured under nonphotorespiratory conditions (ϕ_{int})). Here we also show the calculated intrinsic quantum yield for all models to enable model comparisons. The modeled realized quantum yield under our standard conditions when Q = 100 μmol mol^{-1} (ϕ_{real}) is the initial slope of the leaf level A-Q response shown in Fig. 1(a) for our standard conditions where $V_{c,max}$ was set to 60 μmol m^{-2} s^{-1} (and 45 μmol m^{-2} s^{-1} for low nitrogen conditions) and where temperature = 25°C, atmospheric [O_2] = 210 mmol mol^{-1}, C_a = 380 μmol mol^{-1}, VPD = 1 kPa and soil moisture content was at field capacity. NA, not applicable; ND, no data.

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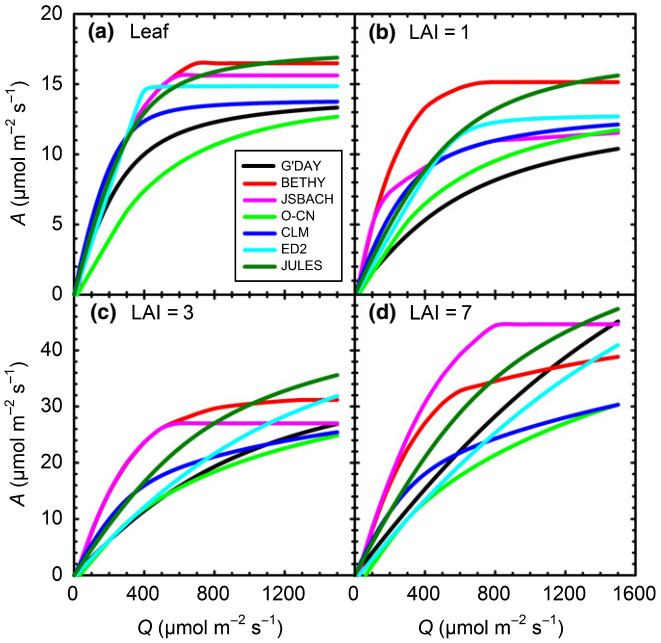

Fig. 1 The response of leaf level (a) and canopy level (b–d) photosynthesis (A) to instantaneous quantum flux density (Q) for three different values of leaf area index; LAI = 1 (b), LAI = 3 (c), and LAI = 7 (d) for seven models; BETHY (red), CLM (blue), ED2 (cyan), JSBACH (pink), JULES (dark green) G'DAY (black), O-CN (light green). Plots show responses in our standard conditions for a single plant functional type, a generic temperate broad leaved deciduous tree. Where maximum carboxylation rate of Rubisco ($V_{c,max}$) is 60 μmol m^{-2} s^{-1}. Vapor pressure deficit (VPD) was fixed at 1 kPa, soil moisture content was fixed at field capacity, and atmospheric [O_2] at 210 mmol mol^{-1}, atmospheric CO_2 concentration (C_a) at 380 μmol mol^{-1}. Sunlit upper canopy leaf temperature was fixed at 25°C.

Niinemets & Keenan, 2014). As discussed earlier, the Φ_{real} in models depends on several assumptions, not just the Φ_{int}, highlighting the need to better parameterize and test modelled light responses with data from field conditions. For example, most existing measurements have been made within a narrow temperature range (20–30°C) and the scarcity of data collected at low temperature has been highlighted as an important driver of model uncertainty at high latitudes (Dietze, 2014).

Leaf level light-saturated CO_2 uptake (A_{sat}) varies considerably between models (Fig. 1a). The variation in modeled A_{sat} is driven by differences in prescribed Rubisco kinetic constants and their temperature dependencies (see later and Table 2), as well as the C_i, which is dependent on the choice of stomatal model. The inflection point of the light response curve marks the transition between light limitation and light saturation of A. There is a wide range in the Q at which A becomes light saturated and therefore the greatest model divergence in A occurs when some models have light saturated A and others do not (i.e. Q = 400–800 μmol m^{-2} s^{-1}, Fig. 1). In addition to differences in the model representation of light limited and light saturated A, variation in the transition phase is attributable to model structure (Table 1), and when present, parameterization of the convexity term (Θ, Table 2), which determines the relative influence of Φ_{real} or A_{sat} on A at a given Q.

Moving from the leaf to the canopy level, responses to irradiance (Fig. 1b–d) are not only dependent on the factors discussed earlier but also on the method used to scale physiology from the leaf to the canopy level, the representation of the light environment within the canopy, and the partitioning of foliage between sunlit and shaded leaves (Gu *et al.*, 2002; Mercado *et al.*, 2009). As a result, canopy scaling exacerbates existing differences between the TBMs and introduces new structural variation that further diversifies model output (Fig. 1b–d). Canopy scaling is discussed in detail later.

Recommendation: (2) Modeled responses of photosynthesis to light need to be parameterized and evaluated against data from field conditions, particularly at low temperature.

Do not mix and match

One issue that emerged here, but is relevant throughout this paper, is the need to avoid piecemeal approaches to model parameterization. For example, we need to carefully and consistently use kinetic constants and temperature response functions because the models are highly sensitive to them. Any constants and functions used when deriving photosynthetic parameters from data have to be the *same ones* used in the model. For example, if a value of $V_{c,max}$ at 25°C is used in a model, that model must use the same Michaelis–Menten constants (K_c and K_o) and Γ^* (e.g. see Table 2), and the associated temperature dependencies, that were used to estimate $V_{c,max}$ from the original A–C_i response curve as well as the same temperature response function used to scale $V_{c,max}$ from the measurement temperature to 25°C. This problem, that derived parameters depend on the equations used to derive them, introduces error when trying to use the parameters to perform meta-analyses or calibrate models (Medlyn *et al.*, 2002a,b; Dietze, 2014). As we make progress to provide models with richer data sets for use in model parameterization and evaluation, we need to archive our raw gas exchange data so that, for example, new kinetic constants and temperature response functions can be applied to old data, maintaining its value as understanding advances. The estimation of quantum yield provides another example where the assembly of parameters (e.g. Φ_{int}, a, Γ^*, Θ) and approaches (e.g. estimation of low light C_i) is not coordinated and where archived data would be useful.

Recommendations: (3) Models need to make careful and consistent use of kinetic constants and temperature response functions. **(4)** Physiologists should archive their raw data to enable coordinated parameterization and the preservation of their data for future analysis.

Short-term response to temperature

The temperature response of A is complex and dependent on additional variables such as Q and C_i (Fig. 2). The C_i in turn depends on g_s and hence VPD, such that the temperature and VPD

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response of g_s also impacts the shape of the temperature response of A (Medlyn *et al.*, 2002a; Lin *et al.*, 2012). The model by Farquhar *et al.* (1980) suggests that A is Rubisco-limited at low temperature – but note that TPU limitation can limit A in some species at low temperature (Sage & Sharkey, 1987). The decline in A at high temperature (Fig. 2) can be brought about by the temperature dependence of J_{max} and the strong increase in photorespiration and mitochondrial respiration with increasing temperature (Farquhar *et al.*, 1980; von Caemmerer, 2000). High temperature limitations on Rubisco activase could also cause decline in A but this mechanism is currently absent from all these models (Salvucci & Crafts-Brandner, 2004a,b; Sage & Kubien, 2007). The steep decline of A at temperatures above 30°C in the Farquhar *et al.* (1980) model is largely driven by the temperature dependence of J_{max}. This effect needs to be treated with some caution as it may be due to irreversible inhibition in the *in vitro* system, from which the function was derived. June *et al.* (2004) provided a simpler empirical equation for fitting the temperature dependence of J_{max}. The temperature dependence of A is also driven by the choice of kinetic parameters and their temperature dependencies as discussed earlier. Some TBMs use spinach (Jordan & Ogren, 1984) or tobacco (Bernacchi *et al.*, 2001) temperature response functions for $V_{c,max}$ for all species. However, as there are important differences in the response of $V_{c,max}$ to temperature among warm and cool climate plant species (Kattge & Knorr, 2007; Galmés *et al.*, 2015), continued acquisition of temperature response functions from different biomes is critically important. The temperature optimum of A (T_{opt}) depends on environmental conditions such as Q and C_a, with T_{opt} being more pronounced at high Q and C_a (e.g. compare Fig. 2a,c with 2b,d). Here, two models stand out for their temperature responses; unlike the majority of models that show an optimum ~24.5°C, ED2 has an emergent temperature optimum at 16°C, despite a $V_{c,max}$ optimum at 39°C, and JSBACH shows no high temperature limitation on A (Table 1; Fig. 2). It is usual for T_{opt} to shift to a slightly higher temperature as C_a rises (Long, 1991) because at high C_a the rate of photorespiration is reduced, thereby extending the temperature range where positive CO_2 assimilation occurs. The CO_2 effect on T_{opt} is evident in Fig. 2 in a number of the models at both the leaf and canopy level. Here, elevating C_a from 380 to 550 μmol mol^{-1} shifts the T_{opt} up by ~2°C (Fig. 2b,d). Two models do not show this shift in T_{opt}: JSBACH has no T_{opt}, and the T_{opt} for ED2 remains at 16°C despite the increase in C_a from 380 to 550 μmol mol^{-1}.

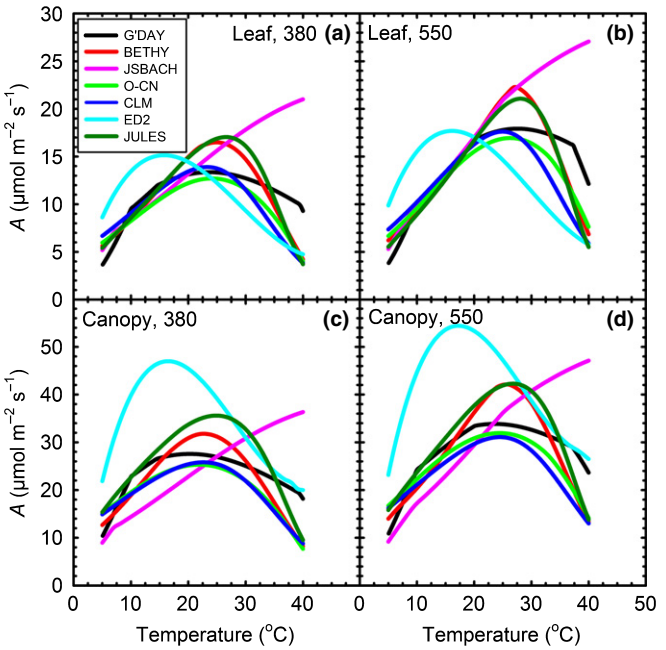

Fig. 2 The response of leaf level (a, b) and canopy level (leaf area index (LAI) = 3; c, d) photosynthesis (A) to leaf temperature at two atmospheric [CO_2] (a, c, 380 μmol mol^{-1}; b, d, 550 μmol mol^{-1}) for seven models; BETHY (red), CLM (blue), ED2 (cyan), JSBACH (pink), JULES (dark green) G'DAY (black), O-CN (light green). Plots show responses in our standard conditions for a single plant functional type, a temperate broad leaved deciduous tree. Where maximum carboxylation rate of Rubisco ($V_{c,max}$) is 60 μmol m^{-2} s^{-1}. Vapor pressure deficit (VPD) was fixed at 1 kPa, soil moisture content was fixed at field capacity, and atmospheric [O_2] at 210 mmol mol^{-1}, instantaneous quantum flux density (Q) at 1500 μmol m^{-2} s^{-1}. Sunlit upper canopy leaf temperature was fixed at 25°C.

Current empirical models predict the response of g_s to temperature based on a relationship between g_s and A that is modified by VPD. This approach is successful in many cases (e.g. Duursma *et al.*, 2014) although the mechanisms underlying the response remain poorly understood (Mott, 2009; Busch, 2013). In addition, there is evidence that the correlation between g_s and A breaks down at high temperatures (> 35°C) in some species, with stomata remaining open while A goes to zero (e.g. Lu *et al.*, 2000; Scafaro *et al.*, 2012; von Caemmerer & Evans, 2015; Teskey *et al.*, 2015; Slot *et al.*, 2016). Presumably this response allows the plant to maintain leaf temperatures at nondamaging levels via transpirational cooling. It is not known how widespread this response is (Teskey *et al.*, 2015) nor to what extent it occurs in the field. Slot *et al.* (2016), for example, find this response in glasshouse-based measurements but not in field trees.

Recommendations: (5) Physiologists need to continue measuring temperature response functions for $V_{c,max}$ and J_{max}. **(6)** More field-based research into the independent temperature response of g_s is required to better understand the mechanism underlying the response of A to high temperatures.

Short-term response to CO_2

At low C_a, when A is limited by the amount of active Rubisco available for carboxylation ($V_{c,max}$), A increases with rising C_a for two reasons: (1) the affinity of Rubisco for CO_2 is low, and therefore increasing the substrate concentration increases carboxylation rates; (2) CO_2 competitively inhibits the oxygenation reaction, reducing CO_2 losses associated with photorespiration (Fig. 3). At higher C_a – i.e. above the inflection point of the A–C_a curve (most notable in the leaf level responses shown in Fig. 3a,b) – A becomes limited by the supply of ATP and NADPH to regenerate the CO_2 acceptor RuBP. At this point A will still rise with increasing C_a, but the CO_2 responsiveness (the increase in A for a given increase in C_a) is reduced as further increases in A are attributable solely to the inhibition of the oxygenation reaction,

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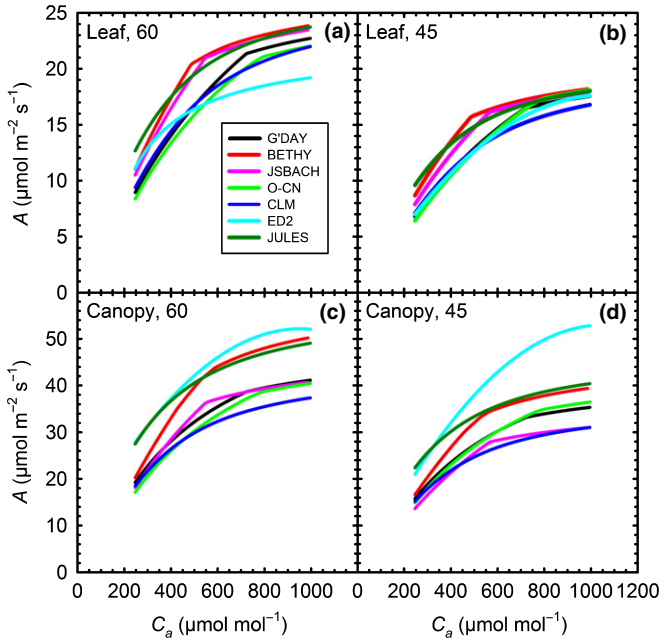

Fig. 3 The response of leaf level (a, b) and canopy level (leaf area index (LAI) = 3; c, d) photosynthesis (A) to atmospheric [CO_2] (C_a) in seven models; BETHY (red), CLM (blue), ED2 (cyan), JSBACH (pink), JULES (dark green) G'DAY (black), O-CN (light green). Panels show responses in our standard conditions for a single plant functional type, a temperate broad leaved deciduous tree where maximum carboxylation rate of Rubisco ($V_{c,max}$) = 60 μmol m^{-2} s^{-1} (a, c) and when $V_{c,max}$ = 45 μmol m^{-2} s^{-1} (b, d). The vapor pressure deficit (VPD) was fixed at 1 kPa, soil moisture content at field capacity and instantaneous quantum flux density (Q) at 1500 μmol m^{-2} s^{-1}, atmospheric [O_2] at 210 mmol mol^{-1}. Sunlit upper canopy leaf temperature was fixed at 25°C.

which increases the availability of ATP and NADPH for RuBP regeneration (Long, 1991; Long *et al.*, 2004).

The shape of the A–C_a response curve is a critical model feature that determines the ability of the terrestrial carbon sink to respond to rising C_a and it is affected by model structure and parameterization (Fig. 3; Tables 1, 2). Variation in the initial slope of the A–C_a response is attributable to C_i and the choice of kinetic constants. For this example of a broad leafed deciduous tree PFT in our standard conditions, all models show that light-saturated A appears to be Rubisco limited (RuBP saturated) below a C_a of 500 μmol mol^{-1} (Fig. 3). As a result the CO_2 responsiveness of A below a C_a of 500 μmol mol^{-1} is similar for all models. However, as C_a rises above 500 μmol mol^{-1} differences in model structure and parameterization lead to substantial variation in CO_2 responsiveness. Three models (CLM, ED2 and JULES) stand out for smooth response curves that lack a clear inflection point (most noticeable in Fig. 3a). All three models adopt the co-limitation approach described by Collatz *et al.* (1991) which smooths transitions between Rubisco limited and RuBP limited A (Collatz *et al.*, 1991; Foley *et al.*, 1996; Clark *et al.*, 2011; Oleson *et al.*, 2013; Table 1). This approach contributes to the greater CO_2 responsiveness at higher C_a observed in CLM and JULES (Fig. 3a). In addition, the four models that lack this smoothing function (BETHY, G'DAY, JSBACH and O-CN) have a marked inflection point between Rubisco limited and RuBP limited A, but the C_a at which this inflection occurs spans a large range (~300 μmol mol^{-1}; Fig. 3) contributing to the variation in CO_2 responsiveness above 500 μmol mol^{-1}. The variation in C_a at which the inflection point occurs has several causes, but the main drivers of this variation are the choice of kinetic constants (~60 μmol mol^{-1}, Table 2), the JV_{ratio}, which for a fixed $V_{c,max}$ sets the inflection point C_i (~125 μmol mol^{-1}, Table 2) and the stomatal model, which determines the C_a at which the inflection point C_i is reached (~175 μmol mol^{-1}; Table 1).

As $V_{c,max}$ is reduced (Fig. 3b,d), the responses of A to changes in C_a are qualitatively similar but model divergence is constrained. Model variation in canopy level responses to rising C_a (Fig. 3c,d) is also attributable to different approaches to canopy scaling as discussed later. The differences seen here in CO_2 responsiveness are substantial – highlighting the impact of different model representations of the FvCB equations, stomatal model choices and the need to better understand controls on the inflection point of the A–C_a response. The C_a at which the inflection point occurs drives uncertainty in the CO_2 stimulation of A at the C_a that will be experienced in the second half of the century, and it is at this higher C_a where model uncertainty is greatest. This model divergence in inflection point probably contributes to the model differences in GPP reported in the recent Free Air CO_2 Enrichment (FACE) model-intercomparison project (Zaehle *et al.*, 2014).

Recommendation: (7) We need improved understanding and model evaluation of the controls on the inflection point of CO_2 response curves.

Short-term response to VPD

Increasing VPD causes stomatal closure, which decreases C_i. The magnitude of the decrease in A resulting from lower C_i is determined by the shape of the A–C_i response as described earlier and shown in Fig. 3. Figure 4 shows the response of A to VPD; model divergence increases with rising VPD, largely due to differences in the parameterization of VPD sensitivity among models. The strong sensitivity of the CLM seen in Fig. 4 is due to the use of RH in the model formulation, and the fact that RH must drop dramatically to obtain increasing VPD with constant temperature, as shown in this plot. There are some models, of which JSBACH in this study is an example, that do not incorporate a stomatal response to RH or VPD (Table 1; Fig. 4). Such formulations were necessary when driving data sets for atmospheric humidity were not available. Given advances in the understanding of stomatal responses and the availability of appropriate driver datasets, stomatal response to RH or VPD should be adopted. However, we believe that formulations involving VPD, such as those adopted by ED2, G'DAY and JULES (Table 1) are theoretically preferable because, unlike RH, VPD is directly proportional to water loss, more closely reflects stomatal mechanics (e.g. Aphalo & Jarvis, 1991; De Beeck *et al.*, 2010), and is strongly linked to productivity (Lobell *et al.*, 2014; Ort & Long, 2014). In addition, formulations involving VPD, rather than RH, will likely be better able to project the response of vegetation to future climate

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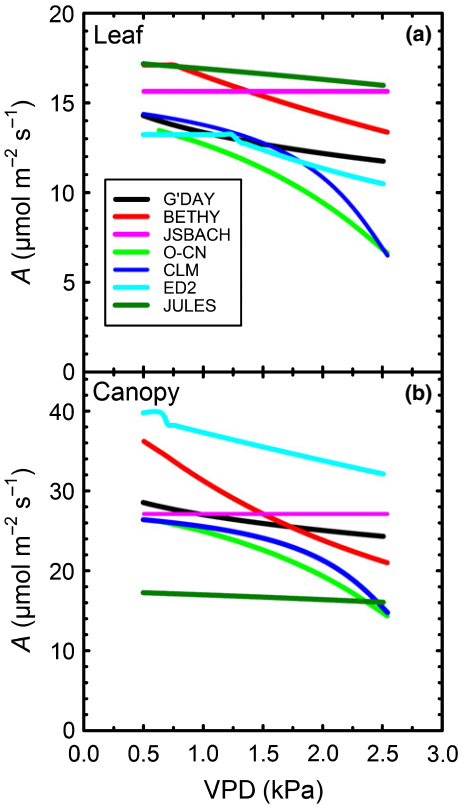

Fig. 4 The response of leaf level (a) and canopy level, where leaf area index (LAI) = 3 (b) photosynthesis (A) to vapor pressure deficit (VPD) for seven models; BETHY (red), CLM (blue), ED2 (cyan), JSBACH (pink), JULES (dark green) G'DAY (black), O-CN (light green). Plots show responses in our standard conditions for a common plant functional type, a temperate broad leaved deciduous tree. Where maximum carboxylation rate of Rubisco ($V_{c,max}$) = 60 μmol m^{-2} s^{-1}. Soil moisture content was fixed at field capacity, instantaneous quantum flux density (Q) at 1500 μmol m^{-2} s^{-1}, atmospheric CO_2 concentration (C_a) at 380 μmol mol^{-1}, atmospheric [O_2] at 210 mmol mol^{-1}. Sunlit upper canopy leaf temperature was fixed at 25°C.

scenarios, because RH is predicted to change little in the future whereas VPD will increase with warming (Sato *et al.*, 2015).

Similar coupled g_s–A models can also be developed from optimization principles. Cowan & Farquhar (1977) proposed that stomatal behavior is optimal when A less the cost of transpiration is maximized, and a number of authors have shown that this theory leads to a relationship between g_s and A that is similar in behavior to empirical formulations (e.g. Hari *et al.*, 1986; Katul *et al.*, 2010; Medlyn *et al.*, 2011). Optimization approaches have the advantage of being based in theory, yielding meaningful parameter values, and providing g_s responses to future environmental conditions where we lack robust measurements, and we encourage their use. However, we also caution that optimization can lead to physiologically incorrect behavior in some circumstances – such as incorrect CO_2 responses, and instability near the transition between Rubisco-limited and RuBP regeneration-limited A – implying that simple, empirically verified equations based on optimization may be more reliable than direct application of numerical optimizations that are also dependent on the careful application of model constraints within TBMs and the optimization approach used.

Large-scale parameterization of stomatal models has been data-limited, with models typically using one nominal set of parameter values for all C_3 vegetation. A major advance in this area was made by Lin *et al.* (2015), who collated a substantial new stomatal conductance database and demonstrated a predicted response of the stomatal slope parameter (g_1) to temperature and consistent differences in g_1 among broadly defined PFTs. This dataset provides a valuable foundation for stomatal model parameterization. However, the coverage of this database is still limited. There is still relatively little information about how g_1 varies among species or genotype, and almost no information on acclimation or plasticity in these parameters in response to abiotic or biotic factors (Way *et al.*, 2011). Models are also sensitive to the minimum stomatal conductance parameter, g_0, particularly under low light and high VPD conditions (Bauerle *et al.*, 2014), but this parameter is poorly quantified.

Recommendations: (8) Models should adopt approaches that include formulations where g_s responds to VPD. **(9)** We need more information about how g_1 and g_0 (or their equivalents) vary among PFTs and in response to environmental drivers.

Short-term response to soil moisture content

Soil moisture availability is a key constraint on A. As soil moisture availability decreases, stomates close, decreasing C_i, and eventually preventing A and transpiration (Fig. 5). Drought can also reduce the biochemical capacity for A, expressed as lower $V_{c,max}$ and J_{max} in models, but the relative balance of these stomatal and biochemical limitations is subject to significant debate (Chaves *et al.*, 2009). Current approaches to modeling the effects of soil moisture on A can be classified into several types: empirical reduction factors; hydraulic limitations; physiological approaches; and a simple supply constraint approach (BETHY). The latter assumes that plant transpiration cannot exceed the potential supply of soil water and that plants can photosynthesize provided there is a sufficient water supply (Table 1).

The empirical reduction factor approach involves multiplying parameters by a soil water stress factor (typically denoted β, ranging from 0 to 1) when soil moisture falls below a given model-dependent threshold. Three of the models in our sample used this approach (CLM, G'DAY and O-CN, Table 1 and Fig. 5). However, there is disagreement among models as to whether the β factor should be applied to the stomatal slope parameter, apparent $V_{c,max}$, or both (De Kauwe *et al.*, 2013). Here, all three models applied the β factor to stomatal model parameters, either the slope (G'DAY and O-CN) or the intercept (CLM), and also to the photosynthetic parameters $V_{c,max}$ (CLM) or $V_{c,max}$ and J_{max} (G'DAY and O-CN; Table 1). Increasing evidence suggests that both stomatal slope and $V_{c,max}$ are affected by low soil moisture, with the reduction in apparent $V_{c,max}$ possibly in part due to lower g_m (Keenan *et al.*, 2010; Egea *et al.*, 2011; Zhou *et al.*, 2013). Several TBMs do include both limitations, but the β factor is tied to the soil water content and therefore models cannot capture the impact of potentially different trajectories of drying and rewetting episodes (Williams & Xia, 2009).

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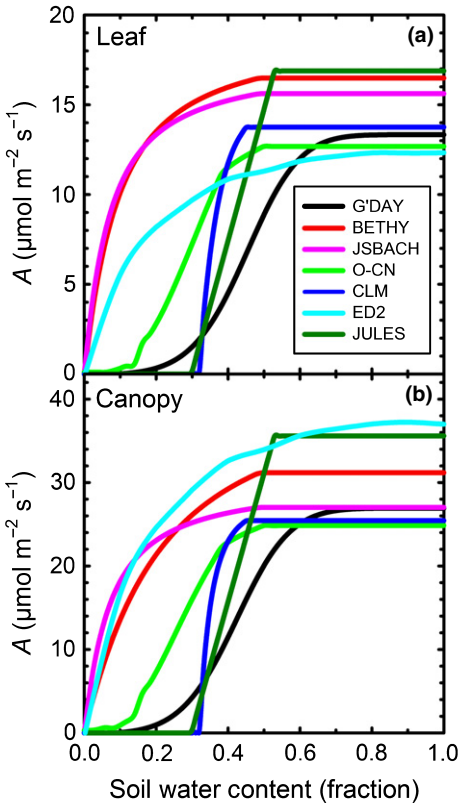

Fig. 5 The response of leaf level (a) and canopy level, where leaf area index (LAI) = 3 (b) photosynthesis (A) to soil water content expressed as a fraction of field capacity for seven models; BETHY (red), CLM (blue), ED2 (cyan), JSBACH (pink), JULES (dark green) G'DAY (black), O-CN (light green). Plots show responses in standard conditions for a single plant functional type, a temperate broad leaved deciduous tree. Where maximum carboxylation rate of Rubisco ($V_{c,max}$) = 60 μmol m^{-2} s^{-1}). Vapor pressure deficit (VPD) was fixed at 1 kPa, instantaneous quantum flux density (Q) at 1500 μmol m^{-2} s^{-1}, atmospheric CO_2 concentration (C_a) at 380 μmol mol^{-1}, atmospheric [O_2] at 210 mmol mol^{-1}. Sunlit upper canopy leaf temperature was fixed at 25°C.

The hydraulic approach offers a number of theoretical advantages over the β-factor approach. Stomatal conductance is modeled as a function of leaf water potential (ψ_{leaf}), which is calculated from soil moisture potential ψ_{soil} and plant and soil hydraulic conductances. There may be a threshold minimum ψ_{leaf} (Williams *et al.*, 1996) or a sigmoidal functional dependence (Tuzet *et al.*, 2003). Implementations also differ on whether responses to VPD are captured by the responses to ψ_{leaf} (Williams *et al.*, 1996; Tuzet *et al.*, 2003) or whether an additional VPD response is also needed (Bonan *et al.*, 2014). The hydraulic approach is appealing to plant physiologists because it reflects some of the key mechanisms thought to influence plant response to drought (Leuning *et al.*, 2004). Because soil hydraulic conductance is assumed to vary with ψ_{soil} this approach also incorporates a dynamic weighting of soil layers whereby lower soil layers become more important as drought progresses (De Kauwe *et al.*, 2015). Furthermore, there is evidence that the photosynthetic response to soil moisture can depend on plant leaf area (e.g. Kelly *et al.*, 2015), an effect that is captured by the hydraulic approach but not the β-factor approach. The chief disadvantage of the hydraulic approach is that it requires additional parameters to represent plant hydraulic conductance and stomatal dependence on leaf water potential. These parameters are not well quantified and can lead to additional uncertainty.

The physiological approaches are based on an understanding of stomatal function and suggest that both metabolic and hydraulic stomatal regulation involves the hormone abscisic acid (ABA), known to promote tolerance against abiotic stress (Jones, 2016). Wilkinson & Davies (2002) proposed a coordinated model of plant responses to stress whereby water stress sensed by the root system stimulates ABA biosynthesis. This signal is then communicated to the guard cells which subsequently induce stomatal closure and reduce water loss. Both roots and leaves synthesize ABA and increasing concentrations of xylem ABA correlate with stomatal closure (Sauter *et al.*, 2001; Wilkinson & Davies, 2002; Christmann *et al.*, 2007).

There are few mathematical descriptions of stomatal control including xylem ABA signaling (Tardieu & Davies, 1993; Dewar, 2002; Huntingford *et al.*, 2015). Tardieu & Davies (1993), combined hydraulic and chemical signaling control of stomatal functioning. The approach of Dewar (2002) is an extension of this approach that also considers xylem embolism and the possible role of combined leaf hydraulic and chemical signaling in addition – or as a possible alternative – to existing root signals. Huntingford *et al.* (2015) revisited the work by Dewar (2002) and provided a g_s formulation which depends on only four variables: soil water content, C_a, evapotranspiration and net A. This is an exciting approach, however there is an acute need for more empirical data to be able to parameterize and evaluate approaches of estimating g_s that include ABA.

The TBMs presented here showed dramatic divergence in the response of A to drought (Fig. 5), with the canopy level responses mostly mirroring the responses seen at the leaf level. Whilst much of this divergence could be explained by the different approaches taken by each model (Table 1), the method used to estimate soil water availability also varies between models. Some models estimate soil water availability using soil moisture content (e.g. O-CN) and others using ψ_{soil} (e.g. CLM). Since soil water retention curves are highly nonlinear and dependent on soil type, this can be a major source of model divergence (Medlyn *et al.*, 2016). From a physiological perspective, ψ_{soil} is thought to be more relevant to plant function than soil moisture content. However, the use of ψ_{soil} can result in unrealistically steep responses to the onset of drought unless it is dynamically averaged over the soil profile (De Kauwe *et al.*, 2016).

Uncertainties in root and stomatal responses are major drivers of TBM uncertainty in predicted Net Primary Production across a wide latitudinal gradient (De Kauwe *et al.*, 2013; Dietze, 2014). Improved model representation of drought responses will require evaluation of underlying mechanisms as well as comparison of high level model outputs to ecosystem fluxes during drought periods. Evaluation of the response of key variables associated with alternative stomatal models against field data is needed. This is challenging as evaluation of alternative mechanisms (e.g. the hydraulic and physiological approaches) requires field level manipulation or exploitation of natural gradients and weather events coupled with substantial campaigns that include parallel

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measurement of many leaf parameters (e.g. ψ_{leaf}, *in situ* gas exchange and $V_{c,max}$) in coordination with plant hydraulic parameters (e.g. soil moisture content, ψ_{soil}, sap flux, hydraulic conductivity and cavitation vulnerability).

Recommendations: (10) Models should respond to soil water availability through ψ_{soil}, but variation in ψ_{soil} with soil depth needs to be incorporated. **(11)** We need rich data sets of coordinated physiological and environmental measurements to enable evaluation of alternative modeling approaches for the representation of the response of A to drought.

Scaling physiology

Earlier, we focused primarily on leaf level responses to environmental and climate change drivers, but a major challenge for model representation is how to scale process knowledge of physiology and leaf level parameterization through time (seasonal change), vertically through the canopy, spatially across the landscape, and also to represent photosynthetic acclimation to rising temperature and C_a. These issues are discussed below.

Effects of day length and season

Photosynthesis responds to short-term environmental changes, but it also shows broad, regular seasonal changes, especially in higher latitudes. In these regions, A halts in the autumn as leaves senesce in deciduous species and decreases as $V_{c,max}$ is down-regulated during the cold winter months in evergreens. Much of this temporal scaling of A is captured in TBMs through phenology models and the direct temperature effects on $V_{c,max}$.

While temperature may be a major factor in driving seasonal patterns of A, other environmental cues may be as, or even more, important. Photoperiod is known to have strong effects on leaf phenology, which has indirect effects on A, but has not generally been considered to affect A directly (Way & Montgomery, 2015). However, Bauerle *et al.* (2012) found that photoperiod was a stronger predictor of seasonal changes in both $V_{c,max}$ and J_{max} than air temperature. In that data set, $V_{c,max}$ peaked immediately after the summer solstice, and declined steadily into the autumn, although air temperatures did not peak until a month or more after the solstice. When this effect was accounted for with a photoperiod correction of $V_{c,max}$ in CLM, the model's ability to capture seasonal patterns of atmospheric C_a was improved (Bonan *et al.*, 2011; Bauerle *et al.*, 2012). Other papers have noted that incorporating a photoperiod scalar with direct effects on $V_{c,max}$ improves estimates of seasonal carbon fluxes in eddy flux studies, supporting a role for photoperiod in modulating $V_{c,max}$ (Medvigy *et al.*, 2013; Stoy *et al.*, 2014). In controlled environments, photoperiod is tightly correlated with total leaf protein content, suggesting a tradeoff between the value of protein and the cost of its maintenance and provides a possible mechanistic explanation for the impact of photoperiod on $V_{c,max}$ (Hannemann *et al.*, 2009). However, not all PFTs show the same response to changes in day length and it is possible that photoperiod corrections may be capturing leaf age effects (Medlyn *et al.*, 2002b, 2007; Busch *et al.*, 2007; Lin *et al.*, 2013; Stinziano *et al.*, 2015). In the tropics, day-length is essentially constant and therefore photoperiod scalars will fail to capture the well documented photosynthetic seasonality associated with tropical evergreen forests (Doughty & Goulden, 2008). Recent work has shown that higher canopy level photosynthetic capacity associated with new leaf flushing can explain the seasonal dynamics of CO_2 uptake in Amazonian evergreen forests (Wu *et al.*, 2016a).

Recommendations: (12) We need to elucidate the mechanism underlying the use of photoperiod scalars to modify photosynthetic parameterization. **(13)** In order to capture photosynthetic seasonality in tropical evergreen forests, we need to develop new approaches that are capable of coupling prognostic leaf phenology to photosynthetic capacity.

Acclimation to temperature

The short-term photosynthetic responses to temperature covered earlier are themselves sensitive to the temperatures experienced over longer timescales (days to weeks). This longer-term adjustment, known as temperature acclimation, has been widely reported and recently reviewed (Smith & Dukes, 2013; Way & Yamori, 2014). The phenomenon is commonly observed as a shift in the optimum temperature for A (T_{opt}), which can maximize the A at the growth temperature (Berry & Björkman, 1980; Kattge & Knorr, 2007; Yamori *et al.*, 2014). The mechanistic process of acclimation and its timescale have not been well described, either within or across species. At the slowest and broadest scales, the process of acclimation is constrained by leaf structure and rates of leaf development and turnover. Leaves that develop under one set of conditions are constrained by their existing anatomy from adjusting fully to a new set of conditions (Campbell *et al.*, 2007). Within a leaf, acclimation rates are driven by the rates at which biochemical and physiological processes can adjust.

At the leaf scale, acclimation results from temperature-driven changes in enzyme abundances and isoforms, and of membrane composition (Yamori *et al.*, 2014). At low growth temperatures, the abundance of Rubisco and other photosynthetic enzymes increases, and some plants produce enzymes with different isoforms, which have different kinetic constants. Under high growth temperatures, plants are thought to increase the stability of the thylakoid membrane, and their capacity for increased electron transport. Also, some plants can produce a more heat-stable form of Rubisco (Crafts-Brandner *et al.*, 1997), and increase expression of heat-shock proteins. Growth temperature also affects the temperature response of respiration, with consequences for net A (e.g. Atkin & Tjoelker, 2003; Way & Yamori, 2014); although the acclimation of respiration may affect plant growth more strongly than that of A for some species (Way & Oren, 2010), this topic lies beyond the scope of this paper and has recently been considered elsewhere (Atkin *et al.*, 2015).

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While long-term acclimation of A to temperature has been observed in many species and studies, fewer studies have quantified acclimation at the process level i.e. $V_{c,max}$ and J_{max}. From observed responses, one may expect seasonal variation in the temperature dependence of J_{max} and changes in the JV_{ratio}. Some confirmation of this was provided by Kattge & Knorr (2007) who reanalysed data from 36 (primarily temperate) plants and showed that the optimum temperature of $V_{c,max}$ and J_{max} increased by 0.44°C and 0.33°C per 1°C increase of growth temperature, and that the JV_{ratio} at 25°C significantly decreased with increasing growth temperature. However, temperature acclimation may result from different processes in different species: $V_{c,max}$ and J_{max} measured at 25°C were, on average, unaffected by growth temperature across tree species (Way & Oren, 2010) and showed a wide variation in responses across a broad range of plant growth forms (Way & Yamori, 2014).

The representation of $V_{c,max}$ and J_{max} acclimation based on Kattge & Knorr (2007) has been included in some models (e.g. Raddatz *et al.*, 2007; Ziehn *et al.*, 2011; Arneth *et al.*, 2012; Lombardozzi *et al.*, 2015), and recent work suggests that incorporation of both photosynthetic and respiratory acclimation can alter projections of land carbon storage by 10–40 Pg by the end of the century (Lombardozzi *et al.*, 2015; Smith *et al.*, 2016). However, there is clear indication that species differ in the degree to which they acclimate to temperature (e.g. Yamori *et al.*, 2014), and no formulations have yet been developed that capture this variation across a broad range of PFTs.

Researchers have recorded acclimation of different species occurring over periods lasting from 2 d to nearly 2 wk (e.g. Slatyer & Ferrar, 1977; Björkman & Badger, 1979; Gunderson *et al.*, 2010). Very limited evidence suggests that the exact timescale of acclimation may not be critical for modeled estimates of GPP as long as it is in a range of *c.* 3–45 d (Dietze, 2014) but the issue needs to be evaluated more thoroughly before that assumption is widely adopted. A specific timescale does need to be specified in models to calculate growth temperature, and is straightforward to identify experimentally. Kattge & Knorr (2007) assumed an acclimation period of 30 d, using an average of day and night temperatures, but it is clear that the bulk of biochemical and physiological adjustments happen over a shorter time period.

Recommendations: (14) Physiologists need to measure thermal acclimation of the photosynthetic traits (e.g. $V_{c,max}$ and J_{max}) that drive model outputs rather than thermal acclimation of A. **(15)** We need a better understanding and model representation of thermal acclimation across biomes, specifically the capacity and degree to which species can acclimate, the timescales over which acclimation occurs, and the degree to which temperature acclimation is affected by other environmental variables.

Acclimation to rising [CO_2]

Photosynthetic acclimation to elevated C_a is the reduced stimulation of A that often occurs following long-term growth at elevated C_a (Ainsworth & Rogers, 2007). It is the result of a reduction in $V_{c,max}$ (Rogers & Humphries, 2000; Long *et al.*, 2004; Ainsworth & Long, 2005; Ainsworth & Rogers, 2007; Leakey *et al.*, 2009). Notably, the reduction in photosynthetic capacity typically reduces the magnitude of the stimulation of A without completely eliminating it (Leakey *et al.*, 2009). The acclimation response reduces allocation of N to Rubisco, thereby allowing N resources to be combined with the greater carbon supply from stimulated A at elevated C_a (Drake *et al.,* 1997; Long *et al.*, 2004). In fact, a meta-analysis of Ainsworth & Long (2005) found that the decrease in leaf N content observed at elevated C_a was largely attributable to the decrease in Rubisco. Consequently, the magnitude of any photosynthetic acclimation is tightly coupled to the carbon and nitrogen status, and the source-sink balance, of the plant (Medlyn *et al.* 1999; Rogers *et al.*, 1998, 2009; Ainsworth *et al.*, 2004; Ainsworth & Rogers, 2007; Leakey *et al.*, 2009). For example, in severely N limited systems, acclimation is strong and can be attributed to a nonspecific reduction in leaf N content (Warren *et al.*, 2015), a mechanism that is currently accounted for by some TBMs in this study (Table 1). Acclimation is also strong when the capacity of sinks to use photoassimilate is low, leading to accumulation of leaf carbohydrates and induction of sugar signaling pathways that reduce Rubisco content (Moore *et al.,* 1999). There is evidence for variation in the acclimation response among functional groups that differ in the processes limiting A at ambient C_a (Ainsworth & Rogers, 2007). Acclimation is rarely observed in plants that have Rubisco-limited A at current C_a and elevated C_a. As C_i rises above the inflection point on an A–C_i response curve, A will become RuBP regeneration-limited, and carboxylation capacity will exceed requirements. In this situation, plants grown at elevated C_a typically exhibit photosynthetic acclimation and reduce their investment in Rubisco (Ainsworth & Rogers, 2007).

The TBMs in this review either do not include photosynthetic acclimation to elevated C_a or link it to a nonspecific reduction in leaf N content that is focused on reduced N availability and constrained C : N stoichiometry (Luo *et al.*, 2004). No models currently include representation of the physiological acclimation to elevated C_a described above and widely reported in FACE studies (Long *et al.*, 2004; Ainsworth & Long, 2005; Ainsworth & Rogers, 2007; Leakey *et al.*, 2009). Recent analysis has shown that failing to account for photosynthetic acclimation at elevated C_a leads to an overestimation of yield in soybean (Twine *et al.*, 2013) – a legume where reductions in leaf N content at elevated C_a are theoretically minimal (Rogers *et al.*, 2009). Therefore, the potential for model representation of photosynthetic acclimation to elevated C_a to reduce errors of this type when modeling more N limited systems is likely substantial. In future TBMs we believe it will be important to capture the mechanisms that control physiological acclimation to rising C_a and not just acclimation resulting from reduced N availability. An approach that reduces N allocation to Rubisco when C_a rises beyond the inflection point of PFT-specific CO_2 response curves would be a good first step. However, unlike thermal acclimation, no algorithms

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have been developed to facilitate inclusion of this concept in TBMs despite the substantial research from FACE experiments. Published data from FACE experiments could potentially be used for development and validation of a new approach.

Recommendation: (16) We need to develop new model representations of the physiological acclimation of photosynthesis to elevated $C_{a.}$

Leaf to canopy scaling

Due to the high nonlinearity of photosynthetic responses to light, temperature and VPD, scaling A from leaves to canopy remains an important challenge for models (Jarvis, 1995). Central to this challenge is TBM representation of light penetration and utilization within the canopy's vertical profile and the vertical scaling of physiology within the canopy. Analogous effects arise from within-canopy variations in temperature and VPD, although to a lower degree (Niinemets & Anten, 2009).

Although the average light intensity typically decreases exponentially with increasing cumulative leaf area index through the canopy, the extent of this decline is affected by the optical properties of individual leaves (including albedo) and how these change with canopy depth, season and leaf age, leaf inclination angle distribution and foliage and canopy spatial clumping (Cescatti & Niinemets, 2004; Kobayashi *et al.*, 2007; Chen *et al.*, 2012; Drewry *et al.*, 2014; Disney, 2015; Wu *et al.*, 2016a,b). Furthermore, due to gaps in the canopy, leaves at a given value of cumulative leaf area index can be sunlit or shaded, further complicating the estimation of light at the leaf surface, leaf absorption, and the subsequent numeric integration of canopy-scale photosynthetic, water, and energy fluxes (de Pury & Farquhar, 1997, 1999; Wang & Leuning, 1998; Kobayashi *et al.*, 2012). Here, the models differ in how these scaling issues are addressed (Table 1) and based on how the canopy is considered, they can be broadly divided between multi-layer models and big-leaf models.

Several TBMs have used the 'big leaf' approach where a canopy approximately represents a single big leaf with a single set of traits describing the photosynthetic capacity together with characteristic light and temperature response functions (generally by PFT), typically scaled to the canopy as a function of leaf area index (e.g. Amthor, 1994; Sands, 1996). Although sometimes still used (e.g. G'DAY; Table 1), the big leaf model approach consisting of a single 'leaf' has been demonstrated to be prone to major integration errors due to lack of consideration of sunlit and shaded leaf area classes (de Pury & Farquhar, 1997; Friend, 2001). These errors were somewhat reduced by developing the 'two big-leaf' model approach, which consists of separate handling of a representative sunlit and a shaded big leaf (de Pury & Farquhar, 1997; Chen *et al.*, 1999; Dai *et al.*, 2004). Indeed, separate integration of A for sunlit and shaded leaf fractions provides a much more accurate integration of carbon and water fluxes (de Pury & Farquhar, 1997; Dai *et al.*, 2004), and this is the approach used in several contemporary TBMs (Table 1).

Big leaf models differ in how whole-canopy $V_{c,max}$ and J_{max} values are derived (or sunlit and shaded big leaf values are derived), but typically, proportionality of photosynthetic capacity and average light (deemed optimal) is assumed (Table 1; Amthor, 1994; Sands, 1995a,b). Yet, such optimality is not present in nature (Niinemets, 2012). In fact, the decline of photosynthetic capacity through the canopy is much shallower than that for light (Lloyd *et al.*, 2010; Dewar *et al.*, 2012; Niinemets *et al.*, 2015). Such departures from optimality have been considered in some multi-layer models (Table 1), but nevertheless, only a few datasets have been used to develop global parameterizations for multi-layer models (e.g. Carswell *et al.*, 2000; Lloyd *et al.*, 2010). PFT and biome-dependent within-canopy acclimation patterns have recently been highlighted (Niinemets *et al.*, 2015) and could be used in future model development.

Depending on the distribution of foliage inclination angles and spatial clumping, the probability for light penetration varies at a given cumulative leaf area index (Cescatti & Niinemets, 2004; Disney, 2015). Importantly, characteristic canopy features differ among PFTs given fundamental differences in leaf habit and growth forms (Cescatti & Niinemets, 2004), as a result of land-use, landscape legacies and past disturbance, but few TBMs take this into account. While the multi-layer models can be easily modified to incorporate different clumping and foliage inclination angles, this is much less straightforward for the big leaf models. In fact, differences in canopy architecture are part of the whole-canopy $V_{c,max}$ and J_{max} values in current big leaf models, i.e. the input values get converted to canopy-scale sunlit and shaded values blurring the definition of $V_{c,max}$ and J_{max} and making comparison with measured leaf level values impossible. Moreover, leaf optical properties and foliar traits change markedly within the vertical canopy profile (Serbin *et al.*, 2014; Wu *et al.*, 2016b; Yang *et al.*, 2016), but are often assumed static, which will generally lead to improper representation of light interception and utilization. This improper representation will feed forward to the integration of leaf energy balance and carbon uptake. We argue that traits like $V_{c,max}$ and J_{max} should retain their original physiological definition and that more effort is needed to improve the representation of canopy architecture and subsequent scaling of foliar properties in TBMs. Modifications to the underlying radiative transfer model (RTM) structure and scaling can help to improve the representation of the canopy light environment and modeling of carbon, water, and energy fluxes (Kobayashi *et al.*, 2012), however increasing RTM complexity or vertical layering should not come at the cost of the ability to parameterize the model. A promising means to constrain these approaches is through model-data integration whereby remote sensing observations (e.g. optical, LiDAR) from the leaf to landscape are used to inform the RTM structure and to parameterize across spatial and temporal scales (e.g. Shiklomanov *et al.*, 2016).

Recommendations: (17) TBMs should not use single layer big leaf models. **(18)** We need better model representation of canopy architecture and vertical scaling of foliar properties, and data to evaluate alternative radiative transfer models and scaling approaches.

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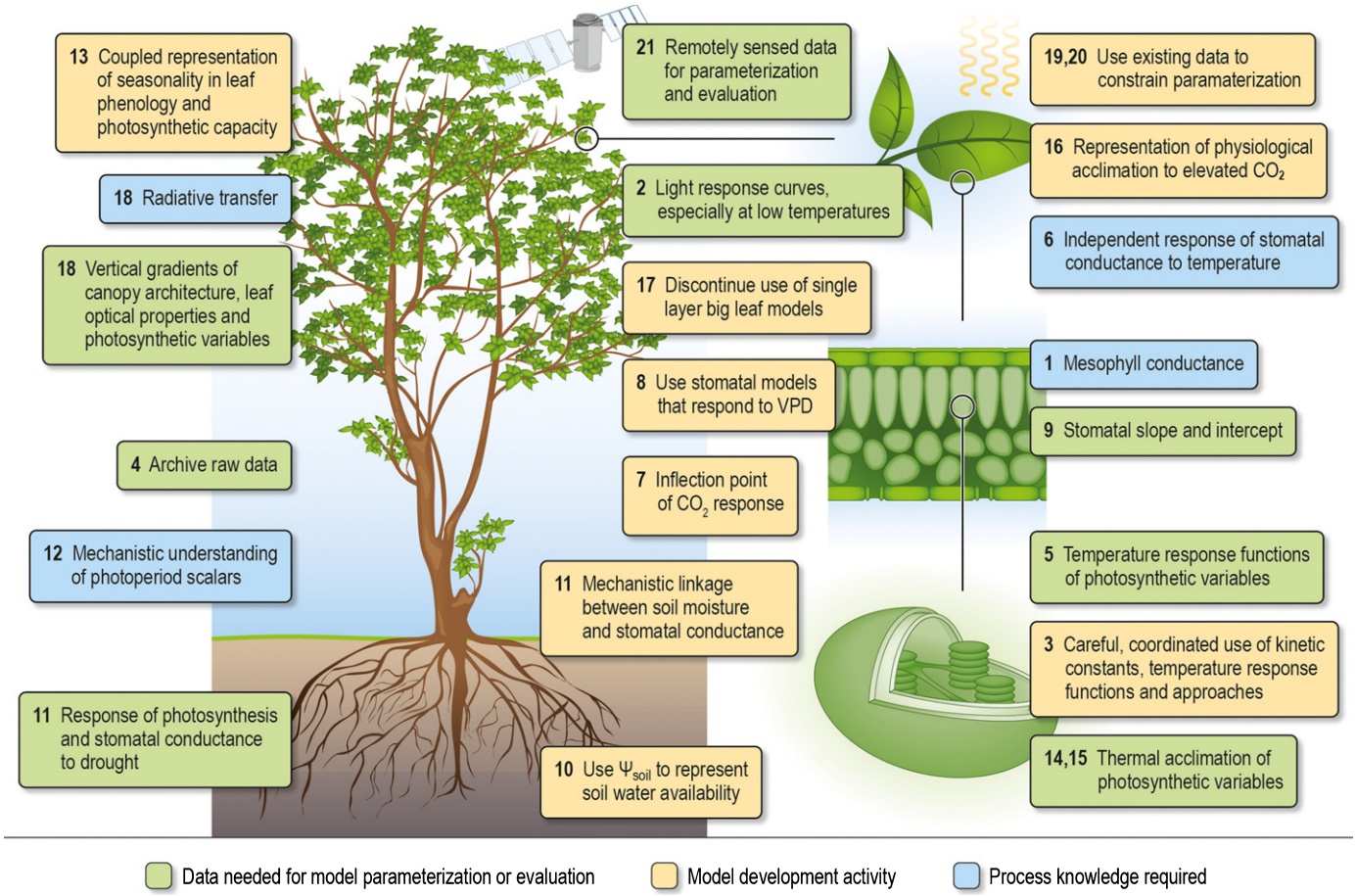

Fig. 6 Summary of the main areas of scientific activity required to advance representation of photosynthesis in Earth system models. Blue boxes show areas where fundamental research is required to advance understanding before incorporation into models. Yellow boxes show areas where model refinement or development is required to improve process representation. Green boxes highlight areas where data are needed to parameterize models or are required to evaluate alternative approaches. The numbers in the boxes are keyed to our recommendations in the text.

Canopy to landscape scaling

There is considerable variability in plant physiological traits across space and time (Serbin *et al.*, 2015; Singh *et al.*, 2015), even within an individual species or PFT (Kattge *et al.*, 2011; Serbin *et al.*, 2014). This variability is driven by differences across vegetation types, photosynthetic pathways, plant successional status, as well as a result of nutrient availability and other abiotic factors. There is a propensity for strong covariance among many key physiological traits as well as fundamental tradeoffs which determine the distribution of these properties across landscapes. Moreover, the nonlinearity in the scaling of model processes from leaf to larger regions requires careful consideration of model parameterization in order to effectively capture the larger-scale emergent responses (Fisher *et al.*, 2015). Parameterization with single, fixed values of photosynthetic capacity likely obscures the true response of vegetation to global change across landscapes, particularly at the current climatic extents of vegetation, thus inadequately capturing critical plant threshold responses to factors such as temperature and precipitation. The links between leaf-level observations, environmental responses and emergent landscape-scale parameterizations needed for TBMs is are not straightforward, and as such global parameterizations are commonly derived through the inversion of large-scale datasets (e.g. Kattge *et al.*, 2009; Lin *et al.*, 2015). However, use of such data sets can yield parameterization that is inconsistent with current model structures resulting in unrealistic model outputs (e.g. Bonan *et al.*, 2012). Furthermore, the tradeoffs among variables (e.g. $V_{c,max}$ vs N) are themselves scale-dependent, with slopes changing depending on whether one is looking at an across-PFT evolutionary constraint, a within-PFT community response, or a within-individual phenotypic response (Feng & Dietze, 2014). Care must be taken to not use data constraints at one scale (e.g. global) to drive responses at another scale (e.g. responses to change over time).

The increasing use of trait databases (Wright *et al.*, 2004; Kattge *et al.*, 2011) in modeling activities has started to address some of these issues by leveraging more comprehensive descriptions of traits within models and across PFTs (LeBauer *et al.*, 2013; Dietze, 2014; Fisher *et al.*, 2015). These databases should also be used to more extensively explore trait-environment relationships. New, model-

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data integration frameworks (e.g. LeBauer *et al.*, 2013; Dietze, 2014) can be used to explore the capacity to adequately parameterize existing and new model representations, expand PFT descriptions, as well as identify critical model uncertainties and data gaps and thus prioritize observational and model development activities (Dietze, 2014). Given the current diverse methods used to parameterize photosynthetic parameters (Rogers, 2014), the available data (e.g. Kattge *et al.*, 2011), and new opportunities to markedly expand databases (e.g. Serbin *et al.*, 2012; De Kauwe *et al.*, 2016), we recommend that models should now use common parameterizations for photosynthetic parameters e.g. $V_{c,max}$ and J_{max} that are constrained by the available data and consistent with known trait covariance, thereby removing unnecessary uncertainty from model projections.

The capacity to utilize remote sensing observations to inform model parameterizations, representations, and trait-environment relationships across spatial and temporal scales is increasing (Dahlin *et al.*, 2013; Serbin *et al.*, 2015; Schimel *et al.*, 2015; Shugart *et al.*, 2015; Singh *et al.*, 2015). Importantly, remote sensing observations can provide a synoptic view of trait variability and functional diversity across landscapes (e.g. Dahlin *et al.*, 2013; Asner *et al.*, 2015; Singh *et al.*, 2015) and identify emergent relationships that could be included in next-generation trait-based models. These observations can also be used as important datasets to benchmark prognostic traits at the relevant spatial scales (e.g. Fisher *et al.*, 2015). Proposed and upcoming satellite missions, including NASA's Hyperspectral Infrared Imager (HyspIRI) mission concept (Lee *et al.*, 2015) and the European Space Agencies Environmental Mapping and Analysis Program (EnMAP; Guanter *et al.*, 2015), will provide a critical capacity to provide this information for global-scale models.

Recommendations: (19) Data constraints (e.g. trait tradeoffs) must be applied at the relevant spatial and temporal scales. **(20)** Where possible, TBMs should use common parameterization for photosynthetic parameters. **(21)** TBMs should make better use of remote sensing data to inform model parameterizations and test predictions.

Conclusion

Realistic model representation of *A*, and more broadly, plant physiological processes, should be an essential component of TBMs because that same plant physiology is determining the response of the terrestrial biosphere to global change, including the fate of the terrestrial carbon sink. However, many TBMs fail to accurately represent photosynthetic responses to key environmental variables. Here, in a subset of TBMs, we have shown marked model divergence in the representation of key physiological responses for a single well-defined PFT. We have made 21 recommendations that highlight where steps can be taken to improve existing model representation. Our recommendations include areas where immediate steps could be taken, areas where model development is hindered by a lack of physiological data and several important avenues of research that are critical to our understanding that are not currently mature enough to include in model structures. These recommendations are summarized in Fig. 6.

Current model representation of *A* has a foundation in research conducted in temperate climates. However, other biomes that are climatically sensitive and globally important are understudied, and therefore process representation in these biomes is uncertain; the Arctic and tropics deserve particular attention. The approach taken here, i.e. evaluating how TBMs reproduce physiological responses to key environmental drivers, was found to be extremely informative by all who participated. We feel the process provides a useful template for meaningful collaboration between empiricists and modelers and that including the physiological outputs considered here as readily available diagnostic features would be a highly valuable addition in new TBMs. This study also highlighted the need for a multi-assumption model framework within which the modeling community and domain experts could evaluate different model structures and parameterization approaches and quantitatively evaluate their effect on model outputs. Such a framework would provide a forum where modelers and, in this case, physiologists could reach agreement over the best approaches for representing and parameterizing the sub-processes within complex TBMs.

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Author contributions

A.R., B.E.M. and J.S.D. initiated the study. G.B., M.C.D., B.E.M., L.M.M., S.P.S., S.S. and S.Z. provided model output. All authors contributed ideas, analyzed data and provided written input. A.R. wrote the manuscript with input from all authors.

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Key words: carbon dioxide CO_2, light, soil water content, stomatal conductance, temperature, terrestrial biosphere models, vapor pressure deficit (VPD).

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