



# Tansley insight

## Evaluating the kinetic basis of plant growth from organs to ecosystems

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### Summary

Understanding how temperature influences the scaling of physiological rates through levels of biological organization is critical for predicting plant responses to climate. Metabolic theory predicts that many rates increase exponentially with temperature following an activation energy ( $E$ ) of 0.32 eV for photosynthesis. Here, I evaluate this prediction for net photosynthesis and organ, individual, and ecosystem growth. Observed  $E$  for photosynthesis varied widely but was not statistically different from predictions, while  $E$  for organs was greater than predicted, and  $E$  for individuals and ecosystems only weakly characterized temperature responses. I review several hypotheses that may underlie these results. Understanding how multiple rate-limiting processes coalesce into a single  $E$  that characterizes metabolic responses to temperature, and how to best estimate  $E$  from unimodal data, remain important challenges.

### I. Introduction

A central challenge of ecology is understanding how climate influences plant metabolism and physiology across scales. Although it has been known for more than a century that metabolism is influenced by temperature (Arrhenius, 1915), predicting emergent outcomes at higher levels of biological organization is more complex. Indeed, understanding how climate influences

metabolism and how this ‘scales up’ to higher levels is a realm of intense research (reviewed in Kooijman, 2010; Yvon-Durocher *et al.*, 2010; Sibby *et al.*, 2012; Maino *et al.*, 2014; Enquist *et al.*, 2015, 2016; Clarke, 2017).

Rates of almost all biological processes increase with temperature to a maximum value at some optimal temperature, and then decrease with temperature above this optimum (Supporting Information Fig. S1) (Johnson *et al.*, 1974). This variation originates from temperature-dependent changes in the collision frequencies and molecular conformations of biochemical reactants and enzymes (Johnson *et al.*, 1974; Kooijman, 2010; Clarke, 2017). However, as many organisms operate within a smaller range of temperatures below their optimal temperature (Savage *et al.*,

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2004; Knies & Kingsolver, 2010; Pawar *et al.*, 2016), the temperature dependence of biological rates  $B$  ( $T^{-1}$ , where  $T$  is the time dimension) is often characterized using the monotonically increasing Boltzmann–Arrhenius model (Gillooly *et al.*, 2001; Kooijman, 2010; Brown & Sibly, 2012), such that

$$B = B_0 e^{-E/kT}, \quad \text{Eqn 1}$$

where  $B_0$  ( $T^{-1}$ ) is a normalization constant,  $k$  is the Boltzmann constant ( $8.617 \times 10^{-5}$  eV  $K^{-1}$ ), and  $E$  (eV) is an effective activation energy that characterizes the temperature dependence of the rate under consideration. The operating temperature  $T$  (K) is the temperature at which the biological processes are occurring—for example, leaf temperature for rates of photosynthesis. The Boltzmann factor  $e^{-E/kT}$  gives the fraction of molecules that attain the activation energy  $E$  needed to react. Equation 1 is mechanistic in the sense that it characterizes the temperature dependence of biochemical reactions. However, it is also phenomenological in the sense that while it is strictly applicable to a single reaction between ideal gases, it is usually applied at higher levels of biological organization.

## II. Predictions for metabolic kinetics

Equation 1 has been successful in characterizing the temperature dependence of biological processes spanning many orders of magnitude in time and space, from subcellular organelles to entire ecosystems (Brown *et al.*, 2004; Brown & Sibly, 2012; Sibly *et al.*, 2012). Building from Eqn 1, metabolic theory (MT) hypothesizes that biological rates will vary with temperature with activation energies  $E$  that are characteristic of rate-limiting reactions. For respiration-dependent processes, MT predicts  $E = 0.65$  eV (Gillooly *et al.*, 2001). This prediction was supported in recent analyses of diverse taxa, although there was substantial variation around this value (Dell *et al.*, 2011).

For photosynthesis-dependent processes, such as plant growth and production, MT predicts  $E = 0.32$  eV (Allen *et al.*, 2005). As the kinetics of net photosynthesis are determined by multiple rate-limiting processes (Sage & Kubien, 2007; Bernacchi *et al.*, 2009), Allen *et al.* made several simplifying assumptions. Specifically, they assumed that photosynthesis can be characterized as  $C_3$ ; is limited by Rubisco-catalyzed carboxylation ( $V_{\text{cmax}}$ ); and occurs at operative temperatures below the optimal temperature for photosynthesis. The prediction for  $E$  was then calculated using a model for carboxylation-limited  $C_3$  photosynthesis (Farquhar *et al.*, 1980) parameterized with empirical activation energies for the four model parameters (Bernacchi *et al.*, 2001). Thus, several kinetic processes coalesce into a single prediction of  $E = 0.32$  eV, which has been hypothesized to apply generally to photosynthesis and many higher-level plant processes (Brown *et al.*, 2004; Allen *et al.*, 2005; Brown & Sibly, 2012).

We should expect  $E$  to differ from this MT prediction whenever the assumptions of Allen *et al.* (2005) are violated. For example, for operative temperatures above the photosynthetic optimum, photosynthesis becomes limited by the maximum rate of electron transport,  $J_{\text{max}}$  (Farquhar *et al.*, 1980; Sage & Kubien, 2007), inactivation of Rubisco (Crafts-Brandner & Salvucci, 2000), and

stomatal closure (Sage & Kubien, 2007; Bernacchi *et al.*, 2009; Slot & Winter, 2017), all with unique temperature dependencies. Further, the MT prediction is based on Rubisco kinetics for a single species (Bernacchi *et al.*, 2001), but recent analyses show that these vary widely among taxa (Galmés *et al.*, 2015, 2016). It is unclear how well a single rate-limiting reaction for a single species characterizes photosynthetic kinetics across a broad range of operative temperatures and taxa.

In the following sections, I assess the kinetic basis of plant growth. First, I evaluate MT predictions for photosynthesis by fitting a unimodal temperature response model to net photosynthesis data. This approach implicitly combines multiple rate-limiting processes and provides a more integrated view on photosynthetic kinetics. Second, I evaluate the kinetics of plant growth at three levels of organization: organs, individuals, and ecosystems. Third, I review several mechanisms that may underlie observed differences in growth kinetics.

## III. Kinetics of net photosynthesis

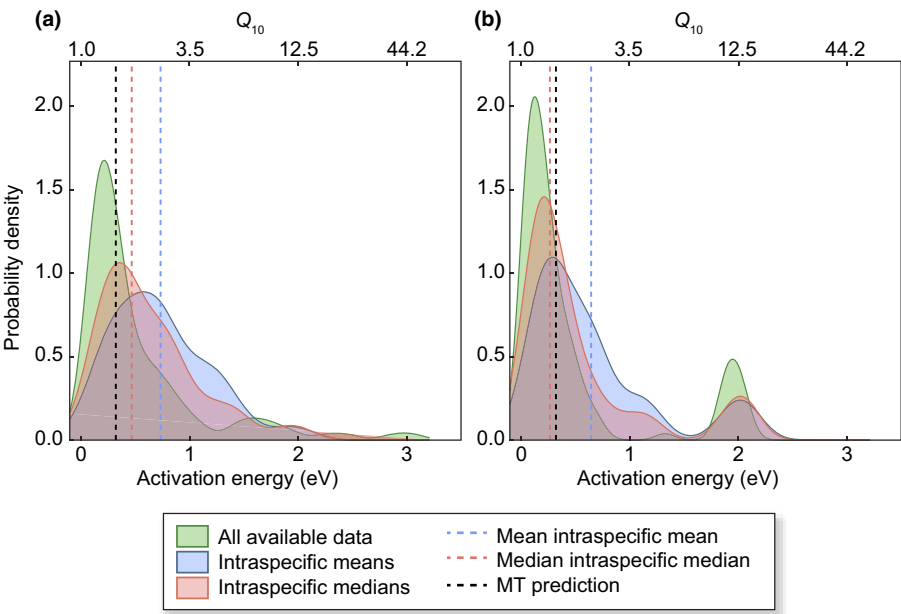
I estimated  $E$  using Sharpe–Schoolfield model fits (Schoolfield *et al.*, 1981) to net photosynthesis data. This model assumes that reaction rates obey Boltzmann–Arrhenius kinetics at lower temperatures, but are reduced by enzyme inactivation at higher temperatures. The Sharpe–Schoolfield model gives the net photosynthesis rate  $A$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) as

$$A = A_0 e^{-E/kT} \left[ 1 + \left( \frac{E}{E_h - E} \right) e^{-E(1/kT_h - 1/kT)} \right]^{-1}, \quad \text{Eqn 2}$$

where  $A_0$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is a normalization constant and  $E_h$  (eV) characterizes enzyme inactivation above the temperature  $T_h$  (K) at which half of the enzymes are nonfunctional. While many biological processes do not meet the strict assumptions of the Sharpe–Schoolfield model, it still provides a useful characterization of thermal performance. Indeed, analogs of Eqn 2 have been widely applied, all the way from biochemical processes of photosynthesis (Farquhar *et al.*, 1980; Medlyn *et al.*, 2002; Bernacchi *et al.*, 2009; Galmés *et al.*, 2015; Stinziano *et al.*, 2018) to ecological and evolutionary patterns and processes (Dell *et al.*, 2011; Parent & Tardieu, 2012; Padfield *et al.*, 2016; Pawar *et al.*, 2016; Schaum *et al.*, 2017).

I fit Eqn 2 to published data for  $C_3$  photosynthesis, yielding 119 fitted curves from 27 species (Methods S1; Figs S2, S3; data described in Michaletz *et al.*, 2016b). Two sets of fits were conducted, with  $E_h$  taken as both a free parameter and a fixed parameter (Methods S1). My aim was to summarize  $E$  across available data, and not to examine the influence of factors such as acclimation, which can have important effects on the temperature response of photosynthesis (Sage & Kubien, 2007; Yamori *et al.*, 2014; Stinziano *et al.*, 2018). This is consistent with a ‘Fermi approach’ for developing intentionally concise and efficient ‘zeroth order’ theory against which complexities can be later evaluated (Harte, 2002; Marquet *et al.*, 2014).

Distributions of  $E$  are shown in Fig. 1. Three distributions are reported for each set of model fits: one based on all data, one based



**Fig. 1** Distributions of activation energies  $E$  for net photosynthesis in 27 species of  $C_3$  plants. Each panel contains three distributions: one based on all available data ( $n = 119$ , green area), one based on intraspecific means ( $n = 27$ , blue area), and one based on intraspecific medians ( $n = 27$ , red area). (a) Distributions estimated from Eqn 2 with  $E_h$  taken as a free parameter. The mean intraspecific mean ( $E = 0.73$  eV, blue dashed line) is significantly greater than the metabolic theory (MT) prediction ( $E = 0.32$  eV, black dashed line), while the median intraspecific median ( $E = 0.47$  eV, red dashed line) has 95% confidence intervals that marginally include the MT prediction. (b) Distributions estimated from Eqn 2 with  $E_h$  taken as a fixed parameter ( $E_h = 2.073$  eV). The mean intraspecific mean ( $E = 0.64$  eV) is significantly greater than the MT prediction ( $E = 0.32$  eV), while the median intraspecific median ( $E = 0.27$  eV) is consistent with the MT prediction. The upper x-axis gives corresponding  $Q_{10}$  values calculated between 20 and 30°C. As explained in Supporting Information Methods S1, these estimates were obtained by fitting Eqn 2 using recent methodology (Dell *et al.*, 2011; Pawar *et al.*, 2016).

on intraspecific means, and one based on intraspecific medians. In accordance with recent findings for disparate rates in diverse taxa (Dell *et al.*, 2011; Parent & Tardieu, 2012), all distributions are right-skewed with wide variation in  $E$ . Since the number of curves available for each species varied substantially (from one to 31 curves

**Table 1** Activation energies  $E$  estimated by fits of Eqn 2 to 119 curves from 27 species of  $C_3$  plants, with  $E_h$  taken as both a free parameter and a fixed parameter

$E_h$ parameterization	Data	Mean $E$ (95% CI)	Median $E$ (95% CI)
Free	All curves ( $n = 119$ )	0.53 (0.42–0.63)	0.30 (0.24–0.37)
	Intraspecific means ( $n = 27$ )	0.73 (0.57–0.90)	0.71 (0.54–0.88)
	Intraspecific medians ( $n = 27$ )	0.63 (0.46–0.80)	0.47 (0.32–0.62)
Fixed	All curves ( $n = 119$ )	0.47 (0.36–0.59)	0.22 (0.17–0.27)
	Intraspecific means ( $n = 27$ )	0.64 (0.43–0.86)	0.42 (0.27–0.56)
	Intraspecific medians ( $n = 27$ )	0.54 (0.31–0.76)	0.27 (0.14–0.39)

Data are summarized as mean and median (95% confidence interval, CI) values for all curves, intraspecific means, and intraspecific medians. Details of Eqn 2 fitting methods, including free and fixed  $E_h$  parameterizations, are described in Supporting Information Methods S1.

per species; Tables 1, S1), the distributions based on all data are weighted heavily towards highly sampled species.

To eliminate this bias, I also present distributions based on intraspecific averages (Fig. 1). Of the averaging approaches used here, medians yield the most representative result as they reduce bias in strongly skewed distributions. For the distributions of medians, median  $E$  values were 0.47 and 0.27 eV for free and fixed  $E_h$ , respectively (Table 1). While these results show that estimated values of  $E$  are strongly influenced by Sharpe–Schoolfield fitting procedures (Methods S1), they nonetheless indicate that between 0 and 30°C, photosynthesis rates generally increase *c.* 1.5-fold for every 10°C increase in leaf temperature. The 95% confidence intervals (95% CIs; Table 1) include the predicted  $E = 0.32$  eV, but  $E$  varies widely and is strongly right-skewed. These differences may reflect the influence of additional temperature-dependent limitations on photosynthesis such as electron transport (Farquhar *et al.*, 1980; Sage & Kubien, 2007), inactivation of Rubisco (Crafts-Brandner & Salvucci, 2000), or stomatal closure (Berry & Bjorkman, 1980; Sage & Kubien, 2007; Bernacchi *et al.*, 2009). These hypotheses should be explored with analyses of larger, more taxonomically diverse datasets.

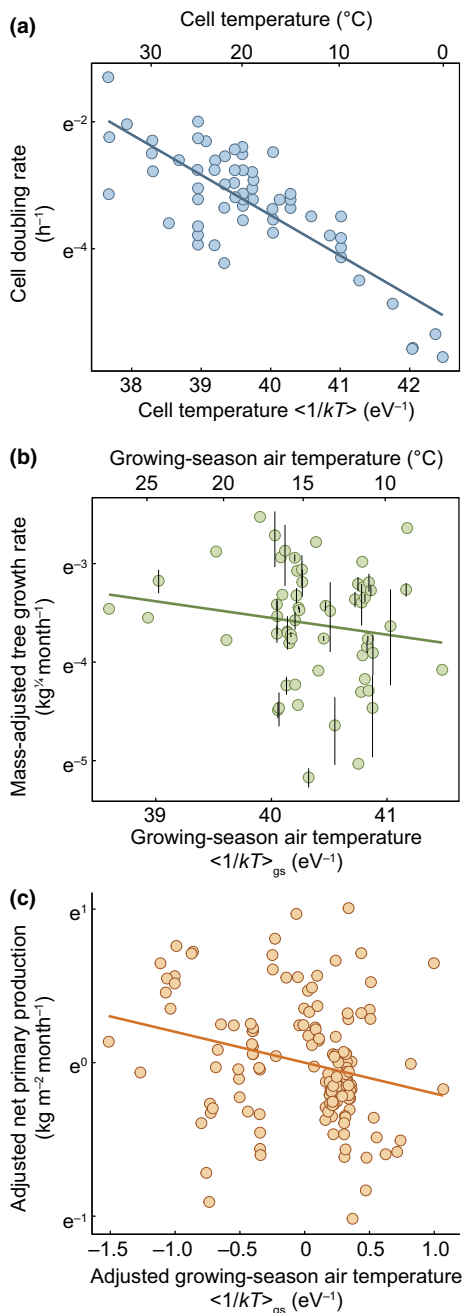
In summary, there is wide variation in  $E$  for net photosynthesis, which probably reflects variation in the relative contributions of rate-limiting biochemical processes and stomatal conductance; averaging matters, and can strongly influence results and interpretations (Fig. 1; Table 1); fitted intraspecific medians are not different from the MT prediction but do vary widely; and estimates of  $E$  are strongly influenced by fitting procedures.

## IV. Kinetics of plant growth

Next I examine the temperature dependence of plant growth at three levels of organization: organs, individuals, and ecosystems (Fig. 2; Table S2; Methods S1). Rates of root organ growth, quantified as meristem cell doubling rates, are shown in Fig. 2(a). Root growth rates varied significantly with temperature ( $P = 4.63 \times 10^{-14}$ ,  $r^2 = 0.63$ ). The fitted  $E = 0.64$  eV had 95% CI (0.51–0.76) that excluded the prediction of 0.32 eV for photosynthesis, but included the prediction of 0.65 eV for respiration. This may reflect a limitation of root growth by respiration in the absence of carbon limitation. Indeed, a current debate questions whether plant growth is carbon source- or sink-

limited (Fatichi *et al.*, 2014; Körner, 2015). Thus, the MT hypothesis that most plant metabolic rates are photosynthesis-limited is not certain and requires further assessment.

Rates of individual tree growth across a broad gradient of growing-season air temperatures are shown in Figs 2(b) and S4. In contrast to results for root growth (Fig. 2a), tree growth was invariant with air temperature ( $P = 0.24$ ,  $r^2 = 0.02$ ). Additionally, the fitted  $E = 0.17$  has a 95% CI =  $-0.12$ – $0.46$ , which includes the MT prediction of 0.32 eV for photosynthesis but excludes the prediction of 0.65 eV for respiration.



**Fig. 2** Modified Arrhenius plots showing relationships between plant growth and temperature at three levels of biological organization. These plots linearize the relationship between growth and temperature to yield a slope  $-E$  that is equal in magnitude but opposite in direction to the activation energy  $E$  (Eqn 1). Temperatures are quantified as  $1/kT$  ( $\text{eV}^{-1}$ ), where  $k$  ( $8.617 \times 10^{-5} \text{ eV K}^{-1}$ ) is Boltzmann's constant and  $T$  (K) is air temperature. All plots control for biomass (described below for each panel; Supporting Information Methods S1), which is critical since biomass is a dominant driver of variation in plant growth and production (Enquist *et al.*, 2016). Specifically, the normalization constant  $B_0$  in Eqn 1 can be unpacked to reveal the influence of biomass  $M$ , such that  $B = B_1 M^\alpha e^{-E/kT}$ , where  $B_1$  is a biomass-independent normalization constant and  $\alpha$  is a scaling exponent that can assume different values but is generally  $c. 3/4$  (Sibly *et al.*, 2012). (a) Relationship between root organ growth (meristem cell doubling rate) and root temperature ( $n = 60$ ). Cell doubling rate varied significantly with cell temperature ( $P = 4.63 \times 10^{-14}$ ,  $r^2 = 0.63$ ). The fitted  $E = 0.64$  eV had 95% confidence intervals (0.51–0.76) that excluded the values of 0.32 eV hypothesized for photosynthesis (Allen *et al.*, 2005) but included the value of 0.65 eV hypothesized for respiration (Gillooly *et al.*, 2001). Biomass effects on growth are controlled for in this analysis, as cell size is essentially constant (within orders of magnitude). Cell doubling time was taken as the mean across all cells in the meristematic region. Data were compiled from  $c. 50$  references (Körner, 2003) as described in Methods S1. (b) Tree growth rates at 59 sites spanning a broad air temperature gradient. Tree growth rate was invariant with air temperature ( $P = 0.24$ ,  $r^2 = 0.02$ ). The fitted  $E = 0.17$  has 95% CI =  $-0.12$  to  $0.46$  which includes the values of 0.32 eV hypothesized for photosynthesis (Allen *et al.*, 2005), but excludes the value of 0.65 eV hypothesized for respiration (Gillooly *et al.*, 2001). Tree growth rates are expressed as mass-adjusted rates,  $BM^{-3/4} = B_1 e^{-E/kT}$ , from rearrangement of the above equation. Mass-adjusted rates are estimates of total (above- plus below-ground) biomass growth, and are plotted as means  $\pm 1$  SE when multiple measurements were available for a single site (see also Fig. S5). As described in Methods S1, air temperature data are monthly averages (including day and night) calculated over growing-season months as described in Kerkhoff *et al.* (2005). All data were obtained from Enquist *et al.* (2007). (c) Net primary production (NPP) at 138 sites spanning a global air temperature gradient. Air temperature explains very little of the global variation in net primary production ( $P = 3.27 \times 10^{-3}$ ,  $r^2 = 0.06$ ). The fitted  $E = 0.20$  has 95% CI =  $0.07$ – $0.33$  which marginally includes the values of 0.32 eV hypothesized for photosynthesis (Allen *et al.*, 2005), but excludes the value of 0.65 eV hypothesized for respiration (Gillooly *et al.*, 2001). NPP includes both above- and below-ground production. Monthly NPP ( $\text{kg m}^{-2} \text{ month}^{-1}$ ) is used here because comparison of metabolic kinetics across sites requires that rates be calculated over the growing season when plants are metabolically active (Michaletz *et al.*, 2018). This panel is a partial regression plot that shows the correct relationship (slope and variance) between NPP and temperature while controlling for the influence of biomass, age, and precipitation (Michaletz *et al.*, 2014); adjusted data for NPP and temperature are partial regression residuals based on this larger multiple regression model. As described in Methods S1, air temperature data are monthly averages (including day and night) calculated over growing-season months as described in Michaletz *et al.* (2014). All data from Michaletz *et al.* (2016a).



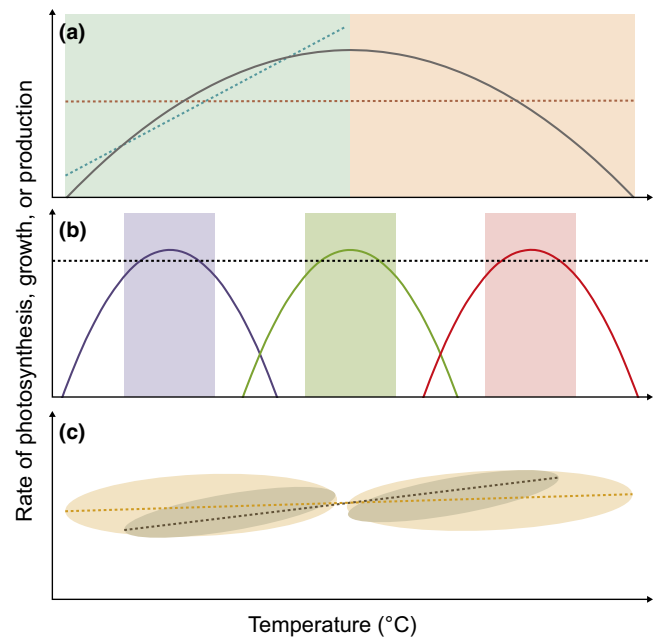
Rates of terrestrial ecosystem net primary production across a global gradient of growing-season air temperatures are shown in Fig. 2(c). Air temperature explains little of the global variation in production ( $P = 3.27 \times 10^{-3}$ ,  $r^2 = 0.06$ ). The fitted  $E = 0.20$  has a 95% CI (0.07–0.33) that marginally includes the prediction of 0.32 eV for photosynthesis, but excludes the prediction of 0.65 eV for respiration. Remarkably, this fitted  $E$  is almost identical to the value of  $E = 0.21$  eV recently observed across a tropical elevation gradient (Enquist *et al.*, 2017).

In summary, the growth kinetics of root organs (Fig. 2a) are consistent with MT predictions for respiration, whereas those for individuals (Fig. 2b) and ecosystems (Fig. 2c) are consistent with MT predictions for photosynthesis (Fig. 1; Table 1). However, for both growth and production, the confidence intervals on  $E$  are wide and air temperature explains < 6% of the observed variation; thus, air temperature is a very poor predictor of variation in plant growth and ecosystem production within this MT approach.

## V. Hypotheses for higher-level kinetic decoupling

What mechanisms might drive observed differences between the kinetics of photosynthesis and higher-level plant growth? Three hypotheses are outlined in Fig. 3. First, plants might violate the MT assumption that operative temperatures are lower than photosynthetic optima (Figs S5, S6). Fitting a monotonically increasing function such as the Boltzmann–Arrhenius model to unimodal data will yield a shallower activation energy, as shown in Fig. 3(a) (see also Knies & Kingsolver, 2010; Dell *et al.*, 2011). If growth and production exhibit a unimodal relationship with air temperature, as recently suggested (Wang *et al.*, 2017), a Boltzmann–Arrhenius fit would yield an apparent invariance of growth and production with air temperature.

Second, acclimation and adaptation of photosynthetic traits might help maximize growth and production across broad temperature gradients (Fig. 3b; Michaletz *et al.*, 2015, 2016b). Acclimation reflects relatively short-term phenotypic changes (e.g. alloenzyme production), whereas adaptation refers to long-term genotypic differentiation (e.g.  $C_3$ ,  $C_4$  and CAM pathways). Both acclimation and adaptation can increase physiological returns at the prevailing plant operative temperature (Kooijman, 2010). The importance of acclimation and adaptation for photosynthesis is extensively documented (Berry & Bjorkman, 1980; Sage & Kubien, 2007; Way & Yamori, 2014; Yamori *et al.*, 2014; Stinziano *et al.*, 2018). For example, biochemical acclimation to cold temperatures may increase rates of plant physiology and offset variation in growth across temperature gradients (Atkin & Tjoelker, 2003; Enquist *et al.*, 2007). Assuming, then, that the optimal temperature for photosynthesis is acclimated or adapted to the average leaf operating temperatures at a given site, which has strong empirical support (Slatyer & Morrow, 1977; Berry & Bjorkman, 1980; Körner & Diemer, 1987; Huxman *et al.*, 2003; Yamori *et al.*, 2014; Slot & Winter, 2016), then even a strong within-site temperature dependence of photosynthesis (such as observed in Fig. 1 and Table 1) would yield an approximate invariance of growth and production across climate gradients. Recent analyses strongly support this hypothesis (Enquist *et al.*, 2017; Malhi *et al.*, 2017).



**Fig. 3** Conceptual diagrams illustrating three hypotheses for observed differences between kinetics of plant growth, ecosystem production, and metabolic theory (MT) predictions for photosynthesis. (a) Average leaf temperatures may often exceed the optimal temperature for photosynthesis, violating the Boltzmann–Arrhenius and MT assumptions of monotonicity and yielding an activation energy  $E$  that is shallower than expected for photosynthesis. In this scenario, rates of carbon assimilation or biomass growth exhibit a unimodal temperature response (solid black line), but the correct  $E$  is only observed from regression (dashed green line) of leaf temperature data that are lower than the optimal temperature for photosynthesis (green area). A shallower  $E$  is observed from regression (dashed orange line) of leaf temperature data that are both lower than (green area) and greater than (orange area) the optimal temperature for photosynthesis. (b) Acclimation or local adaptation of metabolism may dampen thermal response across broad temperature gradients. In this scenario, within-site temperature responses of metabolism (solid lines) are matched to the range of plant operative temperatures (colored areas) at different sites (blue, green, pink). Thus, while photosynthesis, growth, or production varies with temperature within sites, regression of data across sites (dashed black line) yields an apparent invariance with temperature. (c) Homeostasis of plant operative temperatures may dampen thermal responses across air temperature gradients. In this scenario, rates of metabolism vary with plant operative temperature (olive line and areas), but not with air temperature (gold line and areas) as a result of homeostasis of plant temperatures across air temperature gradients (Michaletz *et al.*, 2015, 2016b). This homeostasis rescales temperature data from plant values (olive areas) to air values (gold areas), yielding a relative invariance of photosynthesis, growth, or production with air temperature.

Third, a decoupling of plant and air temperatures may lead to a homeostasis of plant temperatures across air temperature gradients (Fig. 3c). Many ecological analyses, including those in Fig. 2(b) and (c), use air (not plant) temperatures (Michaletz *et al.*, 2014, 2018). However, recent analyses for diverse taxa and growth forms have shown that plant temperatures are buffered relative to air across a gradient of  $c. 60^{\circ}\text{C}$  (Michaletz *et al.*, 2015, 2016b; Dong *et al.*, 2017). Additionally, long-term photosynthetically weighted estimates of leaf temperature are relatively stable across a tropical to subarctic air temperature gradient (Helliker & Richter, 2008;

Michaletz *et al.*, 2016b). This suggests that most photosynthesis occurs at similar operative temperatures across macroecological scales of time and space. This temperature homeostasis originates from the interaction of climate variables and leaf thermal properties within energy budgets. If thermal properties and leaf temperatures vary systematically across temperature gradients, as suggested by this hypothesis, it could drive an apparent dampening in the temperature response of plant physiology. This does not mean that temperature is unimportant for rates of plant metabolism and physiology, but it suggests that the temperatures of plants, and not only air, are necessary for understanding and predicting plant functioning across broad air temperature gradients.

These are just three among many nonmutually exclusive hypotheses. For example, temperature often covaries with other variables that limit plant growth and production, such as solar radiation, nutrient availability, and water availability (Anderson-Teixeira & Vitousek, 2012; Fyllas *et al.*, 2017). Vapor pressure deficit, in particular, varies with air temperature and has well-documented effects on stomatal conductance, net photosynthesis, growth, and production (Tardieu *et al.*, 2011; Parent & Tardieu, 2012; McDowell *et al.*, 2018). Additionally, scale mismatch of data may obscure the temperature sensitivity of growth (Michaletz *et al.*, 2014, 2018). For example, most annual growth is concentrated into relatively short periods of time (Körner, 2012; Cuny *et al.*, 2015) having temperatures that may not be adequately characterized by growing season averages (Way & Oren, 2010); this is especially relevant to macroecological datasets where different variables are often obtained during different time periods. Future work should assess the importance of these hypotheses.

## VI. Conclusions

For net photosynthesis, free and fixed parameterizations of  $E_h$  in Sharpe–Schoolfield model fits yielded different estimates of  $E$ . This highlights a need for additional studies on how to best estimate  $E$  from unimodal temperature response data. Nonetheless, as fitted  $E$  varied widely ( $E = 1.98 \times 10^{-8}$  to 2.07 eV) with strongly right-skewed distributions, average values did not differ significantly from the MT prediction of  $E = 0.32$  eV (Allen *et al.*, 2005). The MT prediction for photosynthesis was not strongly supported by plant growth data at the organ, individual, or ecosystem level, but multiple hypotheses might explain these differences. MT presents a powerful approach to thermal biology, but understanding drivers of variation in  $E$ , including how multiple rate-limiting processes mechanistically coalesce into a single  $E$ , remains an important challenge.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:



**Fig. S1** A typical temperature response curve for a biological rate.

**Fig. S2** Modified Arrhenius plots of Sharpe–Schoolfield model fits (with  $E_h$  as a free parameter) to photosynthesis temperature response data.

**Fig. S3** Modified Arrhenius plots of Sharpe–Schoolfield model fits (with  $E_h$  as a fixed parameter) to photosynthesis temperature response data.

**Fig. S4** Tree growth rates across a broad air temperature gradient.

**Fig. S5** Distributions of intraspecific optimal temperatures for photosynthesis, estimated from Eqn 2 with  $E_h$  as a free parameter.

**Fig. S6** Distributions of intraspecific optimal temperatures for photosynthesis, estimated from Eqn 2 with  $E_h$  as a fixed parameter.

**Table S1** List of taxa, number of curves per taxon, and primary sources for photosynthesis temperature response data used in analyses

**Table S2** List of growth variables, temperature variables, sample sizes, and primary sources for growth analyses

**Methods S1** Description of data and methods used for analyses.

**Notes S1** R code for fitting the Sharpe–Schoolfield model (TPCfitting\_stm.R).

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