1 Thermal acclimation of leaf respiration consistent with optimal plant function

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44 Main

45 Introduction

46 Terrestrial plant respiration is a major component of the global carbon cycle, releasing
 47 *ca.* 60 Pg C yr⁻¹ to the atmosphere: six times more than anthropogenic CO₂ emissions
 48 from all sources combined (Ciais *et al.* 2014). About half this flux is leaf maintenance
 49 respiration in darkness (R_d) (Atkin *et al.* 2007). R_d is highly temperature-dependent,
 50 following a near-exponential relationship over short time-scales (Heskel *et al.* 2016).
 51 It has been predicted that global warming will increase R_d and accelerate future
 52 climate change via a carbon-climate feedback (Cox *et al.* 2000; Huntingford *et al.*
 53 2013). However, large uncertainties in future carbon cycle responses to warming
 54 persist, likely because model formulations of the temperature responses of
 55 photosynthesis and R_d remain poorly constrained by both theory and observations
 56 (Ziehn *et al.* 2011; Booth *et al.* 2012; Friedlingstein *et al.* 2014).

57 Representations of R_d in most land surface models (LSMs) are based on the
 58 instantaneous temperature response of R_d , governed by enzyme kinetics, relative to a
 59 baseline rate, typically at 25°C ($R_{d,25}$) (Atkin *et al.* 2017). $R_{d,25}$ is commonly assumed
 60 to be proportional either to area-based leaf nitrogen content (N_{area}), or to the
 61 maximum rate of carboxylation at 25°C ($V_{cmax,25}$) (Rogers 2014). Predicting
 62 photosynthetic traits from N_{area} is problematic because a large fraction of leaf N is
 63 contained in cell walls (Onoda *et al.* 2017), and significant fractions are also allocated
 64 to other non-photosynthetic functions including defense, storage and osmoregulation
 65 (Dong *et al.*, 2017). Many models treat $V_{cmax,25}$ and $R_{d,25}$ as constant for each plant
 66 functional type (PFT), but spatial and temporal trait variations within PFTs are to be
 67 expected (Wang *et al.* 2017b) and have been reported (Kattge *et al.* 2011, Atkin *et al.*
 68 2015). Moreover, trait differences observed among PFTs could be caused by
 69 acclimation to different environments, rather than intrinsic properties of PFTs.

70 Experiments have shown acclimation of R_d , such that its response to growth
 71 temperature over a week or longer is shallower than its response to temperature
 72 variation in the short term (Atkin & Tjoelker 2003; Gifford 2003; Smith & Dukes
 73 2013; Aspinwall *et al.* 2016; Drake *et al.* 2016; Reich *et al.* 2016; Scafaro *et al.* 2017).
 74 The acclimation of R_d to growth temperature is also evident in spatial observations

(Atkin *et al.* 2015; Slot & Kitajima 2015), showing a far weaker pole-to-equator gradient than would be expected if field-measured R_d followed the instantaneous response of R_d to temperature. By analysing the temperature responses of R_d in different datasets, Vanderwel *et al.* (2015) demonstrated consistency between the observed spatial pattern of R_d and the acclimation of R_d over time. Similar levels of thermal acclimation of photosynthesis and respiration have been shown to occur in different PFTs (Campbell *et al.* 2007; Smith & Dukes 2017b). Pervasive R_d acclimation implies a weaker positive carbon-climate feedback than implied by the temperature response of enzyme kinetics (i.e. the instantaneous response) (Reich *et al.* 2016; Smith *et al.* 2016; Huntingford *et al.* 2017). Neglecting acclimation in LSMs is thus a potential major source of bias in Earth system model predictions (Smith & Dukes, 2013), as recently demonstrated by Huntingford *et al.* (2017).

Still missing is a theoretical explanation for R_d acclimation. Conclusions from empirical studies alone (Wright *et al.* 2006) remain subject to the limitations of sampled region, observational period and experimental design. A theoretical basis is essential to build confidence in carbon-cycle predictions (Prentice *et al.*, 2015). As advocated e.g. by Marquet *et al.* (2014), theories grounded in first principles have the potential to generate explicit quantitative predictions with few assumptions or unconstrained parameters, providing independent standards for comparison with empirical data. Here, we develop such a theory for R_d acclimation, based on the assumption that the various metabolic functions of R_d are coordinated with photosynthetic capacity, indexed by V_{cmax} . In combination with predictions of optimally acclimated V_{cmax} based on the coordination hypothesis (Chen *et al.*, 1993; Haxeltine & Prentice, 1996; Maire *et al.*, 2012; Togashi *et al.*, 2018) – whereby optimal V_{cmax} is just sufficient to use available resources under current average environmental conditions – our approach allows us to formulate and test the sensitivities of the traits of interest (R_d , V_{cmax}) to temperature, yielding results applicable to all plants.

Our theory is based on the concept of eco-evolutionary optimality, which derives from the premise that natural selection favours efficient resource allocation by eliminating unsuccessful or uncompetitive trait combinations (Givnish 1986a; Tilman 1999). Optimality-based theories have proven predictive power for plant functions

including leaf venation networks (Blonder *et al.* 2017), stomatal behaviour (Cowan 1986; Givnish 1986b; Farquhar *et al.* 2002; Lin *et al.* 2015; Wolf *et al.* 2016; Dewar *et al.* 2018), leaf-level CO₂ drawdown (Prentice *et al.* 2014), phenology (Kikuzawa *et al.* 2013; Xu *et al.* 2017), leaf nitrogen content (Wright *et al.* 2003; Maire *et al.* 2012; Dong *et al.* 2017) and adaptations to elevation (Wang *et al.* 2017a); and ecosystem processes including vegetation succession (Weng *et al.* 2017) and primary production (Keenan *et al.* 2016; Wang *et al.* 2017b). By linking R_d with optimal V_{cmax} acclimation (Box 1), we derive quantitative predictions of the thermal sensitivities of acclimated R_d and V_{cmax} evaluated at the prevailing growth temperature, and at 25°C. Our theory implies that correlations between $V_{cmax,25}$ and N_{area} , and between $R_{d,25}$ and N_{area} primarily reflect the N requirements of metabolism (as implied by the coordination hypothesis) rather than ‘N limitation’ of either V_{cmax} or R_d – that is, the amount of ‘metabolic’ N in the leaf is optimized for current conditions. These predictions are tested using two extensive field observational datasets (Atkin *et al.*, 2015; Smith & Dukes, 2017).

Materials and Methods

Theoretical framework

Leaf dark respiration (R_d) is closely coupled with photosynthetic activity (Hoefnagel *et al.* 1998; Wright *et al.* 2004; Noguchi & Yoshida 2008; Tcherkez 2012). As described by the standard biochemical model of photosynthesis (Farquhar *et al.* 1980), the instantaneous rate of photosynthesis by C₃ plants is limited either by the capacity of the enzyme Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) for the carboxylation of RuBP (V_{cmax}), or by the rate of electron transport for the regeneration of RuBP, which depends on absorbed light and the electron transport capacity (J_{max}). R_d is used to support diverse metabolic processes including protein turnover, phloem loading, the maintenance of ion gradients between cellular compartments, nitrate reduction, and the turnover of phospholipid membranes. Among these, protein turnover is the largest contributor to R_d variation and is expected to scale closely with V_{cmax} , which sets the daily maximum photosynthetic rate achieved by leaves under natural growing conditions (Amthor 2000; Atkin *et al.* 2000; Cannell & Thornley 2000; Bouma 2005).

We start from the assumption that at the prevailing growth temperature, V_{cmax} is proportional to the overall metabolic activity of the leaf, which is supported by R_d . The dimensionless factor b (main text equation (1)) is expected to be constant (for all plants) at a given growth temperature. The value of b at 25°C (b_{25}) has been given as 0.011 (Farquhar *et al.*, 1980) or 0.015 (Collatz *et al.* 1991). A constant b_{25} implies that a certain quantity of respiratory enzymes is required for the maintenance of a certain quantity of Rubisco. Our initial attention therefore focuses on the prediction of optimal V_{cmax} achieved by the acclimation of photosynthetic processes.

We hypothesize that V_{cmax} of leaves at any canopy level acclimates to the current environment so as to be just sufficient to allow exploitation of the average available light. This is the “strong form” (Togashi *et al.*, 2018) of the coordination hypothesis (Chen *et al.*, 1993; Haxeltine & Prentice, 1996; Maire *et al.*, 2012) (contrasted with the “weak form” that assumes that the total metabolic N content of the leaf is prescribed, so only the allocation of N to carboxylation versus electron transport capacities is optimized). The hypothesis leads to a prediction of the ecophysiologicaly relevant (acclimated) values of both R_d and V_{cmax} at the prevailing temperature, i.e. the average growth temperature (T_g). Values of R_d and V_{cmax} at 25°C ($R_{d,25}$ and $V_{\text{cmax},25}$) are related to quantities of enzymes, while values at growth temperature ($R_{d,tg}$ and $V_{\text{cmax},tg}$) are hypothesized to be optimized by the plant. Numerical conversion between values applying to different temperatures is accomplished by applying functions (Kattge & Knorr, 2007; Heskell *et al.*, 2016) that describe how the instantaneous rates increase with temperature due to enzyme kinetics. To achieve the same level of V_{cmax} , a smaller quantity of Rubisco (and therefore a smaller $V_{\text{cmax},25}$) is required at a higher temperature (Fig. 1). The coordination hypothesis predicts acclimated values of $R_{d,tg}$ and $V_{\text{cmax},tg}$ that increase with growth temperature, but less steeply than the responses of enzyme kinetics (Togashi *et al.*, 2018). As a result, acclimated values of $R_{d,25}$ and $V_{\text{cmax},25}$ are predicted to *decline* with growth temperature. Moreover, because the instantaneous responses of R_d and V_{cmax} to temperature are slightly different, these differences have to be compensated by differences in the acclimated responses of $R_{d,tg}$ and $V_{\text{cmax},tg}$.

The reasoning set out above can be represented mathematically, leading to a theoretical derivation of the thermal sensitivities of R_d , V_{cmax} and their ratio (assessed

at both T_g and 25°C) as follows. We first use the coordination hypothesis to predict the fractional sensitivity of $V_{\text{cmax,tg}}$ to growth temperature (denoted β_{aV} , the subscripts a and i here represent the acclimated and instantaneous responses, respectively), which is predicted to be less than the instantaneous response, i.e. $\beta_{\text{aV}} < \beta_{\text{iV}}$. The hypothesized proportionality between R_d and V_{cmax} then links the thermal sensitivity of $R_{\text{d,tg}}$ (β_{aR}) with $V_{\text{cmax,tg}}$, since $\beta_{\text{aR}} = \beta_b + \beta_{\text{aV}}$. Here β_b quantifies the variation of b with temperature, which is due to the slight lower instantaneous thermal responses of R_d (β_{iR}) than V_{cmax} , i.e. $\beta_b = \beta_{\text{iR}} - \beta_{\text{iV}} < 0$. Making use of the general properties of logarithms, $\beta_{\text{aV}25}$ and $\beta_{\text{aR}25}$ are predicted as a secondary consequence of $V_{\text{cmax,tg}}$ and $R_{\text{d,tg}}$ acclimation combined with enzyme kinetics: $\beta_{\text{aV}25} = \beta_{\text{aV}} - \beta_{\text{iV}} = \beta_{\text{aR}25} = \beta_{\text{aR}} - \beta_{\text{iR}} < 0$.

Quantitative predictions

Our approach (Box 1) is based on the assumption that acclimated R_d is proportional to photosynthetic capacity, represented by V_{cmax} , where their ratio (b) may be a function of temperature:

$$R_d = bV_{\text{cmax}} \quad (1)$$

We therefore first explain quantitative predictions of the thermal acclimation of optimal V_{cmax} .

The coordination hypothesis predicts a spatial and temporal pattern in V_{cmax} assessed at growth temperature, reflecting acclimation to the prevailing environmental conditions of an individual leaf. In response to environmental variations, it predicts that V_{cmax} can vary vertically within the canopy, geographically among sites, and temporally with atmospheric CO_2 concentration and climate (Haxeltine & Prentice 1996; Ainsworth & Long 2005; Maire *et al.* 2012). V_{cmax} values have been shown experimentally to acclimate to sustained changes in growth temperature, such that V_{cmax} assessed at growth temperature (hereafter $V_{\text{cmax,tg}}$) increases with growth temperature, while $V_{\text{cmax},25}$ declines, along with the Rubisco amount and the fraction of leaf N allocated to Rubisco (Scafaro *et al.* 2017).

Quantitative predictions of V_{cmax} can be obtained from the co-ordination hypothesis by equating the Rubisco-limited (A_C) and electron transport-limited (A_J) rates of C_3

photosynthesis in the Farquhar *et al.* (1980) model (Wang *et al.*, 2017b). For simplicity, we shall assume that the light response of A_J under natural light conditions is effectively linear up to the point at which A_C becomes limiting, implying that limitation of photosynthesis by $J_{\max}$ under average field conditions is generally avoided (Wang *et al.* 2014; Keenan *et al.* 2016; Dong *et al.* 2017; Wang *et al.* 2017a; Togashi *et al.* 2018). Thus, under field conditions the coordination hypothesis predicts (Dong *et al.*, 2017; Togashi *et al.*, 2018):

$$V_{\text{cmax,tg}} \approx \varphi_0 I_{\text{abs}} (\chi c_a + K) / (\chi c_a + 2\Gamma^*) \quad (2)$$

where φ_0 is the intrinsic quantum efficiency of photosynthesis, which is independent of temperature over the normal range of metabolic activity (Collatz *et al.* 1990), and I_{abs} is the leaf absorbed photosynthetic photon flux density (PPFD). χ is the ratio of leaf-internal to ambient partial pressure of CO_2 , c_a is the ambient partial pressure of CO_2 , Γ^* is the photorespiratory compensation point, and K is the effective Michaelis-Menten coefficient of Rubisco. Γ^* and K are temperature-dependent following Arrhenius relationships measured e.g. by Bernacchi *et al.* (2001). The least-cost hypothesis (Prentice *et al.*, 2014; Wang *et al.*, 2017b) predicts optimal χ as a function of growing-season mean values of temperature (T_g) and vapour pressure deficit (D), and elevation (z). This prediction is quantitatively supported by worldwide measurements of χ across species and environments (Wang *et al.* 2017b). Equation (2) yields estimates of V_{cmax} given χ and field-relevant average values of c_a , temperature and PPFD. The theoretical temperature dependence of $V_{\text{cmax,tg}}$ arises from the separate temperature responses of χ , Γ^* and K . The sensitivity of $V_{\text{cmax,tg}}$ to temperature can be obtained by differentiating equation (2). Evaluating the result under standard conditions ($T_g = 25^\circ\text{C}$, $D = 1$ kPa, $z = 0$, $c_a = 40$ Pa) yields $\beta_{\text{aV}} = 5.5\% \text{ K}^{-1}$ (β_{aV} is the fractional sensitivity of $V_{\text{cmax,tg}}$ to temperature after acclimation: see Box 1 for definitions, Figure 1 for a graphical explanation, and Appendix 1 for derivations). This value derives primarily from the sensitivities of K and Γ^* to temperature ($8.5\% \text{ K}^{-1}$ and $5.4\% \text{ K}^{-1}$, respectively), which depend on their activation energies (Bernacchi *et al.* 2001), and to a lesser extent on the sensitivity of χ to temperature ($0.9\% \text{ K}^{-1}$).

$V_{\text{cmax,tg}}$ is then corrected from T_g to 25°C using the enzyme-kinetic temperature response of V_{cmax} (Kattge & Knorr 2007). Evaluated at 20°C (mean T_g in our dataset), this function yields an instantaneous thermal sensitivity of V_{cmax} of $\beta_{\text{iV}} = 9.9\% \text{ K}^{-1}$,

higher than the acclimated thermal sensitivity ($\beta_{aV} = 5.5\% \text{ K}^{-1}$). The thermal sensitivity of acclimated $V_{\text{cmax},25}$ is predicted as the difference between the thermal sensitivities of V_{cmax} acclimated to the growth temperature ($V_{\text{cmax},\text{tg}}$) and the instantaneous enzyme-kinetic response of V_{cmax} (Box 1: $\beta_{aV25} = \beta_{aV} - \beta_{iV} = -4.4\% \text{ K}^{-1}$).

Heskel *et al.* (2016) provided an estimate of R_d at a reference temperature (T_{ref}):

$$\ln R_{d,\text{ref}} = a + 0.1012T_{\text{ref}} - 0.0005T_{\text{ref}}^2 \quad (3)$$

where a is an empirical constant varying among biomes, representing the natural log of the value of R_d at 0°C . The enzyme-kinetic response of R_d to temperature (β_{iR}) as given by Heskel *et al.* (2016) is $8.1\% \text{ K}^{-1}$ at the mean T_g of the data. The enzyme-kinetic thermal response of R_d is slightly smaller than β_{iV} , and leads to a thermal response of parameter b in equation (1) given by the difference between β_{iR} and β_{iV} ($\beta_b = \beta_{iR} - \beta_{iV} = -1.8\% \text{ K}^{-1}$). This then generates a prediction of $\beta_{aR} = 3.7\% \text{ K}^{-1}$ and $\beta_{aR25} = -4.4\%$, which is the same as β_{aV25} , consistent with the assumption that b_{25} is a constant (Box 1). Derivations are provided in Supporting Information (Appendix 1).

Empirical analyses

Photosynthesis and respiration data

We combined two R_d datasets. GlobResp (Atkin *et al.* 2015) contains measurements of R_d , V_{cmax} , N_{area} and leaf mass per area (LMA) from 899 species at 100 locations across the major biomes and continents, including data from an earlier compilation by Wright *et al.* (2004). LCE (Smith & Dukes 2017a) contains field measurements of leaf carbon exchange (including R_d and V_{cmax}) and leaf chemical traits (including N_{area} and LMA) from 98 species at 12 locations spanning 53° latitude in North and Central America (Fig. S1). R_d measurements in both datasets followed the same protocol. Both were taken on fully expanded leaves in daytime after a period of dark adjustment. Inhibition of respiration in the light was not assessed. V_{cmax} values in GlobResp were estimated by the ‘one-point method’ whereas those in LCE were estimated from full A - c_i curves; these methods give closely similar results (De Kauwe *et al.* 2016). Replicated measurements in LCE on the same species and site were averaged. Juvenile samples were excluded. We index T_g by the mean temperature

during the thermal growing season when temperatures are above 0°C, mGDD₀ (Harrison *et al.* (2010). V_{cmax} and R_d values in both datasets are provided with information about measurement temperatures. The values were adjusted both to mGDD₀ and to 25°C using the relevant kinetic responses, as given by (Kattge & Knorr 2007) and Heskell *et al.* (2016). A global climatology of monthly temperature provided by the Climatic Research Unit at a grid resolution of 10 arc minutes (CRU CL2.0) (New *et al.* 2000) was used to provide estimates of mGDD₀ for each location. Thermal acclimation of R_d should apply to both C₃ and C₄ plants, but our theoretical prediction of V_{cmax} acclimation here is developed for C₃ plants, and we did not include C₄ species in our analysis.

Statistical analysis

To test our predictions of the acclimated thermal sensitivities of R_d and V_{cmax} quantitatively, the R_d and V_{cmax} data (assessed at mGDD₀ and 25°C) were first normalized with site-mean PPFD absorbed by leaves (PPFD_L) before performing the Ordinary Least Squares (OLS) regression against temperature. This normalization is appropriate because V_{cmax} is both predicted (see Appendix 1) and observed to vary in proportion to PPFD (Niinemets & Keenan, 2012). If it were omitted, the positive effect of PPFD on R_d and V_{cmax} would contribute to the fitted slope of mGDD₀ due to the strong correlation between those two variables (Fig. S2). Site-mean PPFD_L was estimated from growing-season total incident PPFD at the top of the canopy (PPFD₀):

$$\text{PPFD}_L \approx f \text{PPFD}_0 / L \quad (4)$$

where f is the fraction of incident PPFD absorbed by the canopy (from SeaWiFS data: (Gobron *et al.* 2006; Kelley *et al.* 2013) and L is the leaf area index estimated from Beer's law:

$$L \approx - (1/k) \ln (1 - f) \quad (5)$$

with $k = 0.5$ (Dong *et al.* (2017). This general approximation is used because we do not have information on the light levels of species occupying different canopy strata. PPFD₀ was calculated from CRU CL2.0 data using SPLASH (Davis *et al.* 2017). We applied OLS linear regression of normalized (and natural log-transformed) R_d and V_{cmax} values against mGDD₀. The resulting slope coefficients are directly comparable

with the thermal sensitivities predicted by theory. To check the impact of the PPFD normalization, we also performed regressions without it. Thermal acclimation of R_d and V_{cmax} was further tested within PFTs, with species assigned to deciduous and evergreen needleleaf and broadleaf trees, deciduous and evergreen shrubs, and C3 herbaceous plants.

To test the hypothesis that R_d is mainly determined by V_{cmax} rather than leaf or soil characteristics, we also included LMA and soil pH as additional predictors in the OLS regression above. LMA carries information on the structural component of plant leaves. Broadly speaking, higher soil pH indicates higher soil fertility (Jenny, 1994; Sinsabaugh & Follstad Shah, 2012), and pH has been shown to influence χ (Wang et al. 2017b). These two covariates were selected to test any potential influences of leaf structure and soil nutrient availability, respectively, on R_d . An estimate of soil pH for each location was extracted from the Harmonized World Soil Database (<http://www.iiasa.ac.at>). We applied Ordinary Least Squares (OLS) linear regression of R_d versus V_{cmax} (standardized to 25°C and to mGDD₀, without transformation) to estimate b_{25} and b directly from the fitted slopes. Relationships of N_{area} with V_{cmax} , R_d , and LMA were also tested by OLS multiple linear regression.

Results

Sensitivity of acclimated R_d and V_{cmax} to growth temperature

The predicted sensitivity of V_{cmax} to growth temperature (β_{av}) was 5.5% K⁻¹ under standard environmental conditions. This value is identical with the fitted regression coefficient of normalized and transformed $V_{\text{cmax,tg}}$ against mGDD₀ (5.6% ± 0.3%: mean and 95% confidence interval, $R^2 = 0.50$) (Table 1, Fig. 2).

The prediction that b should decline with temperature by 1.8% K⁻¹ was consistent with the fitted regressions of the ratio of $R_{\text{d,tg}}$ to $V_{\text{cmax,tg}}$; we observed a small but significant negative response of b to growth temperature with a sensitivity of 2.0% ± 0.3%, while b_{25} was indeed independent of mGDD₀, as predicted (Table 1, Fig. 2). The fitted temperature response of $R_{\text{d,tg}}$ was consistently about 2% less steep than that of $V_{\text{cmax,tg}}$ (Table 1).

The canonical value of $b_{25} = 0.015$, as assumed in the photosynthesis model of Collatz *et al.* (1991), was similar to the fitted value of $b_{25} = 0.014 \pm 0.001$ based on the regression of $R_{d,25}$ with respect to $V_{\text{cmax},25}$ (Table 2). The regression lines of $R_{d,\text{tg}}$ with respect to $V_{\text{cmax},\text{tg}}$ when fitted to data in low ($T_g < 15^\circ\text{C}$), medium ($15^\circ\text{C} < T_g < 25^\circ\text{C}$) and high ($T_g > 25^\circ\text{C}$) temperature classes separately (Fig. S3) became shallower toward higher temperature classes, also consistent with the prediction of a negative response of b to temperature.

The difference between the enzyme-kinetic sensitivities of R_d and V_{cmax} to temperature implies that the sensitivity of acclimated $R_{d,\text{tg}}$ to temperature (β_{aR}) is 1.8% lower than that of $V_{\text{cmax},\text{tg}}$ (β_{aV}), implying a theoretical optimum rate of increase of $R_{d,\text{tg}}$ by 3.7% per degree. These theoretical responses are very close to those seen in the observations, but rather more shallow than the 9.9% and 8.1% K^{-1} predicted for the short-term responses of V_{cmax} and R_d from enzyme kinetics (Fig. 1). Theoretically predicted values of the fractional sensitivities of acclimated $R_{d,25}$ (β_{aR25}) and $V_{\text{cmax},25}$ (β_{aV25}) to temperature are negative ($-4.4\% \text{ K}^{-1}$) and this is consistent with the observed negative responses of $R_{d,25}$ and $V_{\text{cmax},25}$ to temperature seen in the data (Table 1). The observed negative response of $V_{\text{cmax},25}$ to growth temperature is identical ($-4.4 \pm 0.3\% \text{ K}^{-1}$) to our theoretical prediction; the observed response of R_d^{25} ($-4.9 \pm 0.3\% \text{ K}^{-1}$) is marginally larger than the prediction.

Regressions performed without PPFD-normalization (Table S1) showed temperature responses with the same signs (positive for V_{cmax} and R_d at growth temperature, negative at 25°C) but slightly steeper (positive slopes) or shallower (negative slopes) than in the main analyses – as expected due to the confounding of PPFD and temperature effects, which normalization removes. R^2 values were consistently greater in the main analyses, by 6-7% for V_{cmax} and R_d at growth temperature and 11-16% for V_{cmax} and R_d at 25°C .

Thermal acclimation of V_{cmax} within PFTs was shown to be broadly consistent with the universal relationships evident in the whole dataset (Table S2). Consistent with Campbell *et al.* (2007) and Smith and Dukes (2017b), no significant differences in thermal acclimation were found between PFTs with different leaf phenology (evergreen versus deciduous), leaf form (needleleaf versus broadleaf), or life form (trees versus shrubs versus herbaceous plants), although the fitted slope for evergreen

broadleaf trees is higher than predicted. Thermal acclimation of R_d within PFTs shows more variable results. Evergreen broadleaf trees show higher than predicted thermal sensitivities of both R_d and V_{cmax} , but the fitted slope of their ratio versus growth temperature ($-1.8\% \pm 0.4\%$) is identical with our predicted value (-1.8%).

Microclimatic acclimation (Niinemets & Keenan 2012), the likelihood that many measured leaves were at least partially shaded (Keenan & Niinemets 2017), and genetic variations involving different plant strategies may all have contributed to the within-site variations in R_d and V_{cmax} reflected in the vertical scatter of points in Fig. 2. The theory was applied here to predict variations in R_d and V_{cmax} across sites, however, and as much as 45% and 60% variation in the community-mean $R_{d,\text{tg}}$ and $V_{\text{cmax,tg}}$ respectively could indeed be explained by growth temperature – with responses in quantitative agreement with predictions (Table S3).

Relationships between dark respiration and carboxylation capacity

We examined the relationships between R_d , V_{cmax} and other factors, in order to test our hypothesis that R_d is principally determined by V_{cmax} . We found that measured R_d and V_{cmax} were positively correlated in the datasets when normalized either to mGDD₀ ($R^2 = 0.25$) or to a reference temperature of 25°C ($R^2 = 0.16$) (Table 2).

Relationships of dark respiration and photosynthetic capacity to other variables

Relationships of R_d and V_{cmax} to N_{area} were similar in strength when normalized to 25°C ($R^2 = 0.14$ and 0.12) (Table 3), but notably weaker when considered at growth temperature ($R^2 = 0.05$ for $R_{d,\text{tg}}$ and 0.02 for $V_{\text{cmax,tg}}$). LMA and $V_{\text{cmax},25}$ together accounted for 42% variation in N_{area} , but most of this explanatory power coming from LMA (Table 3). Similarly, LMA and $R_{d,25}$ together explained 41% variation in N_{area} , but again most of this explanatory power is due to LMA (Table 3).

Considered on their own, neither LMA nor soil pH provided explanatory power in the variations of R_d and V_{cmax} (whether at 25°C and growth temperature). The inclusion of one or the other in addition to mGDD₀ as a predictor provided negligible increases in explained variance (Table S4).

Discussion

Acclimation of leaf dark respiration follows the acclimation of carboxylation capacity

Farquhar *et al.* (1980) modelled instantaneous R_d at 25°C as a fixed fraction (1.1%) of V_{cmax} at 25°C. Collatz *et al.* (1991) – citing Farquhar *et al.* (1980) – modelled R_d at 25°C as 1.5% of V_{cmax} at 25°C. Our results show that R_d and V_{cmax} are indeed closely related, whether standardized to growth temperature or to 25°C, albeit with substantial scatter around the relationship. Moreover, the coefficient relating $R_{d,25}$ to $V_{cmax,25}$ - estimated from this large global dataset ($b_{25} = 0.014 \pm 0.01$, Table 2) is indistinguishable from the value of 0.015 used by Collatz *et al.* (1991). We also predict a slight negative response of b to temperature due to the difference in the kinetic responses of R_d and V_{cmax} . This expectation is consistent with other studies (De Kauwe *et al.* 2016), and well supported by the finding here of a temperature effect in the regression of b (estimated from the $R_{d,tg}$ to $V_{cmax,tg}$ ratio), but not in that of b_{25} (estimated from the $R_{d,25}$ to $V_{cmax,25}$ ratio). The former provides a value of β_b close to our theoretical value of 1.8% K⁻¹ (Table 1).

Atkin *et al.* (2015) indicated a decline in b_{25} with increasing growth temperature. Their dataset that did not include the LCE data. To compare our analysis with that of Atkin *et al.* (2015), we assessed the response of b_{25} to mGDD₀ after excluding the LCE data. The response of b_{25} to mGDD₀ became significant ($p = 0.0076$) but its sensitivity ($\beta_{b_{25}} = -0.009 \pm 0.003$) was much lower than that of b ($\beta_b = -0.024 \pm 0.003$, $p < 0.001$). Atkin *et al.* (2015) considered the mean temperature of the warmest three-month period as growth temperature (TWQ), whereas here all days with temperature above 0°C are accounted in the growing season – thus growth temperature by our definition (mGDD₀) is lower than TWQ, except for the low and high ends of the scale (Fig. S4). This methodological difference might have contributed to a slightly different conclusion regarding the temperature sensitivity of b_{25} .

Equation (1) would potentially allow predictions of the responses of R_d to other environmental determinants, including vapour pressure deficit, elevation and CO₂, if these too are determined by the environmental responses of V_{cmax} . However, the data currently available do not allow us to test these predictions, due to either the limited environmental range covered by the data (such as elevation or CO₂) or the strong

correlations between potential explanatory variables (including light and temperature, Fig. S2). Nevertheless, our theory provides a simple, first-principles approach to predicting the thermal acclimation of R_d – one of the most important mechanisms missing from current LSMs (Huntingford *et al.* 2017).

Observed temperature responses are consistent with optimal plant function

Many ecosystem models assume that R_d and V_{cmax} respond to temperature following the same functions that are routinely observed in short-term studies, disregarding acclimation. Our results contradict this assumption. Optimally acclimated values of both fluxes do increase with temperature, but much less steeply than expected from short-term responses. Instead it appears that leaves ‘discount’ enzyme-kinetic responses, so the two limiting photosynthetic rates remain similar *under the prevailing growth temperature*. Positive temperature responses arise because of the differential temperature sensitivities of two key quantities – the effective Michaelis-Menten coefficient of Rubisco (K) and the photorespiratory CO_2 compensation point (I^*) – in the Farquhar *et al.* (1980) model. These predictions are supported by the finding of temperature responses in the datasets evaluated here: that is, after the R_d and V_{cmax} values have been corrected to site-specific mean growing-season temperatures, we find responses closely similar to the predicted optimal responses (Fig. 2).

The acclimated sensitivity of dark respiration to warming

Acclimated R_d is predicted to increase with temperature by 3.7% per degree. This long-term (weekly or longer) sensitivity is supported by the data and is smaller than the enzyme-kinetic sensitivity of either R_d or V_{cmax} . This response is generally conservative among PFTs.

Reich *et al.* (2016) conducted outdoor open-air warming experiments on ten boreal and temperate tree species. Whole plants were warmed by 3.4°C during four growing seasons, and showed even stronger acclimation of R_d and an acclimated sensitivity of only 1.5% per degree. Slot and Kitajima (2015) indicated a value of 5.7% for the temperature sensitivity of R_d based on a meta-analysis of 43 independent experiments (mostly short-term, laboratory studies). Our theory predicts β_{dR} as 3.7% per degree warming, intermediate between the values found by Reich *et al.* (2016) and Slot and

Kitajima (2015). In a study that acclimated plants for seven days, Smith and Dukes (2017b) found even less acclimation of R_d than either of those studies. The differences among these three studies suggest that the time scale of exposure to elevated temperatures might play a role.

Heskel *et al.* (2016) presented data from different biomes that can be compared to our predictions of the acclimation of R_d . We can estimate a in equation (3) by rearrangement, with $T_{\text{ref}} = 25^\circ\text{C}$:

$$a = \ln R_{d,25} - 0.1012 \times 25 - 0.0005 \times 25^2$$

$$= \ln b_{25} + \ln V_{\text{cmax},25} - 0.1012 \times 25 - 0.0005 \times 25^2 \quad (6)$$

The thermal sensitivity of a should therefore be the same as that of β_{aR25} . Its decline from tundra to tropical forests (Heskel *et al.*, 2016) is the result of R_d acclimation to growth temperature (Slot & Kitajima 2015; Vanderwel *et al.* 2015). Our theory estimates a independently: $a = -2.502$ when $V_{\text{cmax},25} = 50 \mu\text{mol m}^{-2} \text{s}^{-1}$ (i.e. equivalent to $R_{d,25} = 1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$), or $a = -1.407$ when $V_{\text{cmax},25} = 150 \mu\text{mol m}^{-2} \text{s}^{-1}$ (i.e. equivalent to $R_{d,25} = 4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$). These values are similar to those derived from observations by Heskel *et al.* (2016): lower for warm biomes (e.g. $a = -2.749$ for lowland tropical rainforest), where we would expect relatively low $V_{\text{cmax},25}$; and higher for cold biomes (e.g. $a = -1.604$ for tundra), where we would expect relatively high $V_{\text{cmax},25}$. These values from Heskel *et al.* (2016) allow us to approximate the thermal sensitivity of a as $-4.6\% \text{ K}^{-1}$, assuming a growth temperature range of 25°C from tundra to rainforest – very close to our theoretical prediction of $\beta_{aR25} = -4.4\% \text{ K}^{-1}$.

Relationships of respiration and photosynthetic capacity with leaf N

It is often assumed that R_d and V_{cmax} (assessed at standard temperature) are closely related to N_{area} , and empirical studies have reported relationships of both quantities to N_{area} (Reich *et al.* 1998; Meir *et al.* 2001; Wright *et al.* 2004; Atkin *et al.* 2015). Correlation of both $R_{d,25}$ and $V_{\text{cmax},25}$ with N_{area} is expected because of the significant fraction of N_{area} that is contained in Rubisco and other photosynthetic proteins, and the functional relationship between R_d and V_{cmax} . (N_{area} should always be compared to R_d and V_{cmax} corrected to a common temperature, because the amount of “metabolic”

N required to achieve a given catalytic activity is strongly dependent on temperature.) We found the expected positive relationships of $R_{d,25}$ and $V_{cmax,25}$ to N_{area} , but they were not strong ($R^2 = 0.11$ and 0.14 , Table 3). Onoda *et al.* (2017) noted the substantial fraction of leaf N allocated to cell walls, in addition to the fraction contained in photosynthetic proteins. Our finding that far more variation in N_{area} can be explained by LMA than by V_{cmax} (Table 3) suggests that the structural (cell wall) component of N_{area} is important (see also (Dong *et al.* 2017)). N_{area} is thus not a straightforward predictor of either V_{cmax} or R_d , but rather contains both a metabolic component (related to $V_{cmax,25}$) and a structural component proportional to LMA (Dong *et al.*, 2017). Mass-based quantities show a similar pattern (Table S5) with more variation in N_{mass} explained by LMA than by V_{cmax} . However, LMA is negatively related to N_{mass} , which indicates that the concentration of N in bulk leaf tissue is lower than that in the photosynthetic machinery.

The coordination hypothesis implies that V_{cmax} , and therefore also the metabolic component of N_{area} , should be determined by photosynthetic demand – rather than V_{cmax} being determined by N_{area} , as is currently assumed in many models. This point is further addressed by (Maire *et al.* 2012; Dong *et al.* 2017), who noted that the coordination hypothesis predicts an optimal value for metabolic N_{area} on the basis of environmental conditions alone. The empirical V_{cmax} – N_{area} relationship has been widely interpreted as a manifestation of ‘N limitation’ of photosynthesis at the leaf level (Luo *et al.* 2004), and underpins the use of N_{area} as a predictor of photosynthetic capacity in models (Ciais *et al.* 2014). An alternative interpretation is that leaf metabolic N depends primarily on the demand for photosynthetic capacity, which is set by the local environment and in turn determines the capacity for dark respiration; while N availability primarily influences the allocation of carbon to leaves versus other organs (LeBauer & Treseder 2008; Poorter *et al.* 2012).

Conclusions

The observed thermal acclimation of R_d follows the optimization of V_{cmax} as predicted by the coordination hypothesis. This acclimation dampens the enzyme-kinetic response of R_d to temperature and shows little influence from other factors. The discrepancy between thermal acclimation and enzyme-kinetic thermal response implies that both R_d or V_{cmax} , converted to 25°C or any other arbitrarily chosen

reference temperature, must decline with plant growth temperature. These principles would be straightforward to incorporate in an LSM framework, as an alternative to PFT-based schemes in current use. The theory provides an explanation for the observed correlations between N_{area} , V_{cmax} and R_d that differs from the common assumption that N_{area} determines V_{cmax} and R_d , and supports an alternative perspective on the coupling between the terrestrial carbon and nitrogen cycles.

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Table 1: Summary of Ordinary Least-Squares regressions for natural log-transformed area-based leaf dark respiration (R_d), area-based maximum carboxylation rate (V_{cmax}) and their ratio as a function of growth temperature. Both R_d and V_{cmax} have been standardized to growth temperature ($R_{d,\text{tg}}$ and $V_{\text{cmax,tg}}$) and to 25 °C ($R_{d,25}$ and $V_{\text{cmax},25}$), and normalized by site-mean leaf absorbed photosynthetic photon flux density. The fitted coefficient and its confidence interval are shown together with the corresponding theoretical expectation, the intercept (mean $\pm$ standard error), the coefficient of determination (r^2) and the degrees of freedom (df). Non-significant coefficients are shown in grey.

Quantity	Theoretical value	Fitted coefficient	Confidence intervals		Intercept	r^2	df
			2.5%	97.5%			
$R_{d,\text{tg}}$	0.037	0.033	0.029	0.038	-9.335 $\pm$ 0.051	0.34	1245
$V_{\text{cmax,tg}}$	0.055	0.056	0.050	0.061	-6.386 $\pm$ 0.054	0.50	1009
$R_{d,\text{tg}}/V_{\text{cmax,tg}}$	-0.018	-0.020	-0.026	-0.015	-2.916 $\pm$ 0.060	0.05	1007
$R_{d,25}$	-0.044	-0.049	-0.054	-0.045	-7.261 $\pm$ 0.052	0.25	1245
$V_{\text{cmax},25}$	-0.044	-0.044	-0.049	-0.038	-3.907 $\pm$ 0.054	0.26	1009
$R_{d,25}/V_{\text{cmax},25}$	0	-0.005	-0.010	0.001	-3.317 $\pm$ 0.060	0.00	1007

745 Table 2: Summary statistics for Ordinary Least Squares regressions of area-based leaf
 746 dark respiration (R_d) against area-based maximum carboxylation rate (V_{cmax}) assessed
 747 at growth temperature and at 25°C. The fitted slopes and intercept are shown together
 748 with their standard errors (SE), the coefficient of determination (r^2) and the degrees of
 749 freedom (df).
 750

Formula	Slope	SE	Intercept	SE	r^2	p value	df
$R_{d,\text{tg}} \sim V_{\text{cmax,tg}}$	0.015	0.001	0.495	0.026	0.25	<0.05	1007
$R_{d,25} \sim V_{\text{cmax},25}$	0.014	0.001	0.787	0.048	0.16	<0.05	1007

751 Table 3: Summary statistics for Ordinary Least Squares regressions of area-based leaf
752 nitrogen content against area-based leaf dark respiration (R_d), area-based leaf
753 maximum capacity of carboxylation (V_{cmax}) assessed at growth temperature and 25°C,
754 and leaf mass per area (LMA). The fitted slopes (mean $\pm$ standard error) are shown
755 together with the intercept (mean $\pm$ standard error), the adjusted coefficient of
756 determination (r^2) and the degrees of freedom (df). All variables were natural-log
757 transformed.
758

Coefficient					Intercept	r^2	df
$V_{\text{cmax,tg}}$	$V_{\text{cmax},25}$	$R_{d,tg}$	$R_{d,25}$	LMA			
0.083 $\pm$ 0.019					0.409 $\pm$ 0.059	0.02	935
0.058 $\pm$ 0.015				0.491 $\pm$ 0.021	-1.849 $\pm$ 0.107	0.39	934
	0.242 $\pm$ 0.022				-0.199 $\pm$ 0.081	0.12	935
	0.148 $\pm$ 0.018			0.458 $\pm$ 0.021	-2.055 $\pm$ 0.106	0.42	934
		0.177 $\pm$ 0.022			0.677 $\pm$ 0.015	0.05	1165
		0.107 $\pm$ 0.018		0.508 $\pm$ 0.020	-1.724 $\pm$ 0.097	0.38	1164
			0.301 $\pm$ 0.022		0.590 $\pm$ 0.013	0.14	1165
			0.174 $\pm$ 0.019	0.471 $\pm$ 0.020	-1.606 $\pm$ 0.097	0.41	1164

Figure 1: Schematic of the thermal sensitivities of area-based maximum capacity of carboxylation (V_{cmax}) and leaf dark respiration (R_d). β_{aV} : the acclimated thermal sensitivity of V_{cmax} assessed at growth temperature (T_g). β_{aR} : the acclimated thermal sensitivity of R_d assessed at growth temperature. β_{iV} : the kinetic thermal sensitivity of V_{cmax} assessed at growth temperature. β_{iR} : the kinetic thermal sensitivity of R_d assessed at growth temperature. $\beta_{\text{aV}25}$: the acclimated thermal sensitivity of V_{cmax} assessed at 25°C. $\beta_{\text{aR}25}$: the acclimated thermal sensitivity of R_d assessed at 25°C. β_b : the thermal sensitivity of the ratio of R_d to V_{cmax} assessed at growth temperature. V_{cmax} and R_d are assessed at growth temperature ($V_{\text{cmax},\text{tg}}$ and $R_{\text{d},\text{tg}}$) as a starting point, 25°C as the common practice ($V_{\text{cmax},25}$ and $R_{\text{d},25}$) and a higher growth temperature (T'_g) for the acclimation behaviour ($V'_{\text{cmax},\text{tg}}$, $R'_{\text{d},\text{tg}}$, $V'_{\text{cmax},25}$ and $R'_{\text{d},25}$) to warming.

Figure 2: Natural log-transformed light-normalized leaf dark respiration (R_d), maximum carboxylation rates (V_{cmax}) and their ratio, standardized to growth temperature ($R_{d,\text{tg}}$, $V_{\text{cmax,tg}}$, b : $R_{d,\text{tg}}/V_{\text{cmax,tg}}$) and to 25°C ($R_{d,25}$, $V_{\text{cmax},25}$, b_2 : $R_{d,25}/V_{\text{cmax},25}$), as a function of growth temperature (mGDD_0). Solid blue lines are the fitted lines from Ordinary Least Squares regressions. Solid black lines are theoretical predictions. Dashed lines represent the instantaneous temperature response based on enzyme kinetics.