

1 **Acclimation of leaf respiration consistent with optimal photosynthetic capacity**

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33

34 **Running Title** (A short running title of less than 45 characters including spaces)

35 Optimal acclimation of leaf dark respiration

36 Abstract

37 Plant respiration is an important contributor to the proposed positive global carbon-
38 cycle feedback to climate change. However, as a major component, leaf
39 mitochondrial ('dark') respiration (R_d) differs among species adapted to contrasting
40 environments and is known to acclimate to sustained changes in temperature. No
41 accepted theory explains these phenomena or predicts its magnitude. Here we propose
42 that the acclimation of R_d follows an optimal behaviour related to the need to maintain
43 long-term average photosynthetic capacity (V_{cmax}) so that available environmental
44 resources can be most efficiently used for photosynthesis. To test this hypothesis, we
45 extend photosynthetic co-ordination theory to predict the acclimation of R_d to growth
46 temperature via a link to V_{cmax} , and compare predictions to a global set of
47 measurements from 112 sites spanning all terrestrial biomes. This extended co-
48 ordination theory predicts that field-measured R_d should increase by 3.7% and V_{cmax}
49 by 5.5% per degree increase in growth temperature. These acclimated responses to
50 growth temperature are less steep than the corresponding instantaneous responses,
51 which increase 8.1% and 9.9% per degree of measurement temperature for R_d and
52 V_{cmax} , respectively. Data-fitted regression slopes proof indistinguishable from the
53 values predicted by our theory, and smaller than the instantaneous slopes. Theory and
54 data are also shown to agree that the basal rates of both R_d and V_{cmax} assessed at 25°C
55 decline by ~ 4.4% per degree increase in growth temperature. These results provide a
56 parsimonious general theory for R_d acclimation to temperature that is simpler – and
57 potentially more reliable – than the plant functional type-based leaf respiration
58 schemes currently employed in most ecosystem and land-surface models.

59 Keywords (6-10)

60 acclimation, carbon cycle, carboxylation capacity (V_{cmax}), climate change, co-
61 ordination, land-surface model, leaf mass per area, leaf nitrogen, nitrogen cycle,
62 optimality, photosynthesis

63

64 1 | Introduction

65 Land plant respiration is a major component of the carbon cycle, releasing *ca.* 60 Pg
66 C yr⁻¹ to the atmosphere: six times more than anthropogenic CO₂ emissions from all
67 sources combined ([Ciais et al., 2014](#)). About half is due to mitochondrial respiration
68 in leaves ([Atkin et al., 2007](#)), which is usually called ‘dark’ respiration (R_d) since it is
69 most easily measured in darkened leaves; mitochondrial respiration continues in the
70 light, although at a reduced rate ([Tcherkez et al., 2017](#)). Leaf respiration is closely
71 coupled with photosynthetic activity ([Hoefnagel et al., 1998](#), [Noguchi & Yoshida,](#)
72 [2008](#), [O’Leary et al., 2019](#), [Tcherkez, 2012](#), [Wright et al., 2004](#)). As described by the
73 standard biochemical model of photosynthesis ([Farquhar et al., 1980](#)), the
74 instantaneous rate of photosynthesis by C₃ plants is limited either by the capacity of
75 the enzyme Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) for
76 the carboxylation of RuBP (V_{cmax}), or by the rate of electron transport for the
77 regeneration of RuBP, which depends on absorbed light and the electron transport
78 capacity (J_{max}). R_d of fully developed leaves is used to support metabolic processes
79 including protein turnover, phloem loading, the maintenance of ion gradients between
80 cellular compartments, nitrate reduction, and the turnover of phospholipid membranes.
81 Among these, protein turnover is the largest contributor to variation in R_d . Given that
82 Rubisco is a substantial fraction of total leaf protein, R_d is expected to scale closely
83 with V_{cmax} , which sets the daily maximum photosynthetic rate achieved by leaves
84 under natural growing conditions ([Amthor, 2000](#), [Atkin et al., 2000](#), [Bouma, 2005](#),
85 [Cannell & Thornley, 2000](#), [O’Leary et al., 2019](#)). R_d is commonly assumed in Land
86 Surface Models (LSMs) to be proportional either to V_{cmax} or, alternatively, to area-
87 based leaf nitrogen content (N_{area}) ([Rogers, 2014](#)).

88 Leaf respiration is enzyme-catalysed and therefore temperature-dependent. On a time
89 scale of minutes to hours, R_d responds to leaf temperature near-exponentially and is
90 determined principally by the temperature dependence of the reaction rates of
91 multiple enzymes involved in various respiratory pathways in the cytosol and
92 mitochondria ([Atkin et al., 2005](#), [Atkin & Tjoelker, 2003](#)). We refer to this observed,
93 composite temperature response as the “instantaneous” response. Because of this
94 temperature response of R_d , it has been proposed that global warming will increase
95 plant respiration and accelerate climate change ([Cox et al., 2000](#), [Huntingford et al.,](#)

96 [2013](#)). However, the magnitude of this positive feedback remains unclear. It depends
97 on the sensitivity of plant respiration to temperature changes over longer time scales,
98 which – as many experiments have shown – is damped, relative to the short-term
99 response, by acclimation ([Atkin & Tjoelker, 2003](#), [Reich et al., 2016](#), [Scafaro et al.,](#)
100 [2017](#)). The longer-term response of plant respiration to the prevailing growth
101 temperature is also manifest in spatial patterns of leaf R_d ([Atkin et al., 2015](#), [Slot &](#)
102 [Kitajima, 2015](#)), which show a far less steep pole-to-equator gradient than would be
103 expected from the instantaneous response – a consequence of both acclimation
104 (plastic responses) and adaptation, i.e. differences among genotypes and species
105 adapted to contrasting environments. [Vanderwel et al. \(2015\)](#) moreover demonstrated
106 consistency between the observed spatial pattern of R_d and the acclimation of leaf R_d
107 over time. Pervasive long-term acclimation of respiration implies a weaker positive
108 carbon-climate feedback than is implied by the instantaneous temperature response
109 ([Huntingford et al., 2017](#), [Reich et al., 2016](#), [Smith et al., 2016](#)). Neglecting the
110 acclimation of plant respiration to temperature in LSMs may therefore be a major
111 source of bias in Earth System model predictions ([Huntingford et al., 2017](#), [Smith et](#)
112 [al., 2016](#)).

113 Quantitative explanations and predictions of the acclimation and adaptation of leaf R_d
114 to temperature are still lacking. Conclusions from empirical studies alone ([Wright et](#)
115 [al., 2006](#)) are insufficient to address the underlying causality; a firmer theoretical
116 basis is essential to build confidence in carbon-cycle predictions ([Prentice et al.,](#)
117 [2015](#)). Here we propose a theoretical framework for the acclimation of leaf R_d based
118 on a few key hypotheses. We first assume acclimation of V_{cmax} (Step 1 in Figure 1)
119 via the ‘co-ordination hypothesis’, which states that V_{cmax} assessed at growth
120 temperature ($V_{\text{cmax,tg}}$) has a general tendency to adjust to average daytime conditions
121 so that the electron transport- and Rubisco-limited photosynthetic rates (A_J , A_c) are co-
122 limiting ([Chen et al., 1993](#), [Haxeltine & Prentice, 1996](#), [Maire et al., 2012](#)) (that is, A_J
123 $\approx A_c$). Co-limitation is optimal in an eco-evolutionary sense because any other
124 outcome would either incompletely exploit available light, or require additional
125 respiration to maintain excess amounts of Rubisco. This hypothesis explained 64% of
126 field-measured $V_{\text{cmax,tg}}$ variability in C_3 plants across different biomes, and has been
127 used with success to predict global patterns of primary production ([Smith et al., 2019a](#),
128 [Wang et al., 2017b](#)). Second, the various metabolic functions of R_d in mature leaves

129 are assumed to be tightly coupled to V_{cmax} (Step 3 in Figure 1) – implying a close link
 130 between the acclimation of V_{cmax} and R_d . We test this hypothesis later, alongside the
 131 alternative hypothesis that R_d depends on N_{area} . To simplify the theoretical framework
 132 and mathematical derivations, we (a) disregard any possible differences in the
 133 instantaneous thermal responses of R_d and V_{cmax} among species and across sites (Steps
 134 2 and 4 in Fig 1), and (b) assume infinite mesophyll conductance and non-limiting
 135 electron-transport capacity ([Keenan et al., 2016](#), [Togashi et al., 2018](#), [Wang et al.,](#)
 136 [2014](#)). Although uncertainties are thereby inevitably introduced, these simplifications
 137 allow us to test first-order effects at a global scale, appropriately for the potential
 138 improvement of LSMs.

139 **2 | Materials and methods**

140 **2.1 | Quantitative predictions**

141 Based on the simplifying assumption that leaf R_d adjusts over time primarily to
 142 maintain the turnover of Rubisco and other enzymes involved in the Calvin cycle, we
 143 start from the premise that at the prevailing growth temperature (T_g), the acclimated
 144 $R_{d,tg}$ is proportional to acclimated $V_{\text{cmax},tg}$:

$$145 \quad R_{d,tg} = b_{tg} V_{\text{cmax},tg} \quad (1)$$

146 while recognizing that the proportionality factor b_{tg} could vary with environmental
 147 conditions. We therefore first focus on quantitative prediction of the optimal thermal
 148 acclimation of $V_{\text{cmax},tg}$.

149 **2.1.1 | Step 1: optimal $V_{\text{cmax},tg}$ and its thermal acclimation based on the** 150 **coordination hypothesis**

151 We hypothesize that V_{cmax} of leaves at any canopy level acclimates to the current
 152 environment in such a way that the Rubisco-limited (increasing with V_{cmax}) and
 153 electron transport-limited (increasing with absorbed PPFD) photosynthetic rates tend
 154 to converge. This is the ‘strong form’ of the coordination hypothesis ([Chen et al.,](#)
 155 [1993](#), [Haxeltine & Prentice, 1996](#), [Maire et al., 2012](#)), contrasting with a ‘weak form’
 156 that assumes that the total metabolic N content of the leaf is prescribed so that only
 157 the allocation of N to carboxylation versus electron transport capacities is optimized
 158 (e.g. [Quebbeman and Ramirez \(2016\)](#)). In response to environmental variations, the

159 coordination hypothesis predicts vertical variation of $V_{\text{cmax,tg}}$ within the canopy,
 160 geographic variation among sites, and temporal variations with atmospheric CO₂
 161 concentration and climate ([Haxeltine & Prentice, 1996](#), [Smith et al., 2019b](#), [Terrer et](#)
 162 [al., 2018](#)). Thus, under field conditions the coordination hypothesis predicts that
 163 ([Wang et al., 2017a](#)):

$$164 \quad V_{\text{cmax,tg}} \approx \varphi_0 I_{\text{abs}} (\chi c_a + K) / (\chi c_a + 2\Gamma^*) \quad (2)$$

165 where φ_0 is the intrinsic quantum efficiency of photosynthesis (mol mol⁻¹); I_{abs} is the
 166 PPF absorbed by the leaf (μmol m⁻² s⁻¹); χ is the ratio of leaf-internal to ambient
 167 partial pressure of CO₂ (Pa Pa⁻¹); c_a is the ambient partial pressure of CO₂ (Pa); Γ^* is
 168 the photorespiratory compensation point (Pa); and K is the effective Michaelis-
 169 Menten coefficient of Rubisco (Pa). Γ^* and K are temperature-dependent following
 170 Arrhenius relationships as measured e.g. by Bernacchi et al. ([2001](#)). Acknowledging
 171 that Rubisco kinetics traits vary both within and among species, we applied various
 172 Rubisco catalytic constants (the Michaelis–Menten coefficients for carboxylation and
 173 oxygenation, and the Rubisco specificity factor) provided by ([Galmés et al., 2016](#)) to
 174 estimate the uncertainties (± 1 s.d.) in K , Γ^* and their instantaneous thermal responses.

175 The least-cost hypothesis ([Prentice et al., 2014](#), [Wang et al., 2017b](#)) predicts optimal χ
 176 to be a function of growing-season mean values of temperature (T_g ; K), vapour
 177 pressure deficit (D ; Pa) and elevation (z ; m). These predictions are quantitatively
 178 supported by worldwide measurements of χ across species and biomes ([Wang et al.,](#)
 179 [2017b](#)). Equation (2) then yields estimates of V_{cmax} given χ and field-relevant average
 180 values of c_a (Pa), temperature (K) and PPF ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

181 We define temperature sensitivities (β) of various quantities as fractional increases per
 182 degree. The fractional sensitivity of $V_{\text{cmax,tg}}$ to temperature after acclimation (β_{aV}) can
 183 be deduced by differentiating equation (2) with respect to T_g :

$$184 \quad \beta_{\text{aV}} = (\partial V_{\text{cmax,tg}} / \partial T_g) / V_{\text{cmax,tg}} = \partial \ln V_{\text{cmax,tg}} / \partial T_g$$

$$185 \quad = \partial \ln(\chi c_a + K) / \partial T_g - \partial \ln(\chi c_a + 2\Gamma^*) / \partial T_g \quad (3)$$

186 Evaluating equation (3) under standard conditions ($T_g = 298$ K, $D = 1$ kPa, $z = 0$, $c_a =$
 187 40 Pa) yields $\beta_{\text{aV}} = 5.5 \pm 0.3$ % K⁻¹. This value derives primarily from the sensitivities

188 of K and Γ^* to temperature (8.5% K⁻¹ and 5.4% K⁻¹, respectively), which depend on
 189 their activation energies ([Bernacchi et al., 2001](#)), and to a lesser extent from the
 190 sensitivity of χ to temperature (0.9% K⁻¹).

191 2.1.2 | Step 2: optimal $V_{\text{cmax},25}$ and its thermal acclimation

192 Described by a modified Arrhenius function ([Kattge & Knorr, 2007](#)), the
 193 instantaneous temperature response of V_{cmax} to temperature provides a link between
 194 $V_{\text{cmax,tg}}$ and $V_{\text{cmax},25}$:

$$195 \quad V_{\text{cmax,tg}} = V_{\text{cmax},25} \times f_v$$

196 where

$$197 \quad f_v = e^{H_a(T_g - 298.15) / 298.15 T_g R} \times [1 + e^{(298.15 \Delta S - H_d) / (298.15 R)}] / [1 + e^{(T_g \Delta S - H_d) / (T_g R)}] \quad (4)$$

198 where H_a is the activation energy (71 513 J mol⁻¹), R is the universal gas constant
 199 (8.314 J mol⁻¹ K⁻¹), $T_{\text{ref}} = 298.15$ K, H_d is the deactivation energy (200 000 J mol⁻¹),
 200 and ΔS is an entropy term (J mol⁻¹ K⁻¹), which can be calculated using a linear
 201 relationship with T_g from ([Kattge & Knorr, 2007](#)) with a slope of 1.07 J mol⁻¹ K⁻²
 202 and an intercept of 668.39 J mol⁻¹ K⁻¹.

203 To estimate the uncertainties (± 1 s.d.) in Rubisco kinetics, we applied various
 204 maximum carboxylase turnover rates provided by [Galmés et al. \(2015\)](#). Equation (4)
 205 then generates an instantaneous response of V_{cmax} to temperature with a sensitivity β_{IV}
 206 of 9.9 ± 1.4 % K⁻¹, and allows β_{qV} to be derived as:

$$\begin{aligned} 207 \quad \beta_{\text{qV}} &= \partial \ln V_{\text{cmax},25} / \partial T_g \\ 208 \quad &= \partial \ln V_{\text{cmax,tg}} / \partial T_g - \partial \ln f_v / \partial T_g \\ 209 \quad &= \beta_{\text{aV}} - \beta_{\text{IV}} \\ 210 \quad &= -4.4 \pm 1.4 \text{ \% K}^{-1} \end{aligned} \quad (5)$$

211 We can thus break down the acclimated temperature sensitivity of $V_{\text{cmax,tg}}$ (β_{aV}) into
 212 the instantaneous sensitivity of Rubisco to temperature changes (β_{IV}) and the
 213 acclimated sensitivity (β_{qV}) of the amount of Rubisco (as indexed by $V_{\text{cmax},25}$, the
 214 catalytic activity of Rubisco at 25°C) to growth temperature.

215 **2.1.3 | Step 3: optimal $R_{d,25}$ and its thermal acclimation based on the link to**
 216 $V_{\text{cmax},25}$

217 In commonly used photosynthesis models, leaf $R_{d,25}$ is assumed proportional to
 218 $V_{\text{cmax},25}$ with the ratio given as 0.011 ([Farquhar et al., 1980](#)) or 0.015 ([Collatz et al.,](#)
 219 [1991](#)). This assumption implies that $R_{d,25}$ is related to $V_{\text{cmax},25}$ by a constant factor b_{25} :

$$220 \quad R_{d,25} = b_{25} V_{\text{cmax},25} \quad (6)$$

221 and thus also that $\beta_{qV} = \beta_{qR}$ (Figure 1).

222 We test this key assumption in parallel empirical analyses. The effects of other
 223 potential influences, including leaf mass per area, leaf nitrogen content and soil
 224 properties, on $R_{d,25}$ are also tested.

225 **2.1.4 | Step 4: optimal $R_{d,gt}$ and its thermal acclimation**

226 [Heskel et al. \(2016\)](#) provided an empirical formula to estimate R_d at 25°C:

$$227 \quad \ln R_{d,25} = a + 0.1012 \times 25 - 0.0005 \times 25^2 \quad (7)$$

228 where a is an empirical constant varying among biomes, representing the natural
 229 logarithm of the value of R_d extrapolated to 0°C. The instantaneous response of R_d to
 230 temperature (β_{iR}) as given by [Heskel et al. \(2016\)](#) is 8.1% K⁻¹ at the mean T_g of the
 231 data. β_{iR} is slightly smaller than β_{iV} , and leads to a response of parameter b_{tg} in
 232 equation (1) given by the difference between β_{iR} and β_{iV} ($\beta_b = -1.8\% \text{ K}^{-1}$). This then
 233 generates the predictions $\beta_{qR} = -4.4\% \text{ K}^{-1}$ and $\beta_{aR} = 3.7\% \text{ K}^{-1}$.

234 Using other instantaneous thermal response curves (for example, equations 1 and 3 in
 235 [Atkin et al. \(2015\)](#), equation 1 in ([Reich et al., 2016](#)), and equation 1 in [Kattge and](#)
 236 [Knorr \(2007\)](#)) yielded slightly different instantaneous responses of R_d and V_{cmax} to
 237 temperature. However, those changes also effect the temperature adjustment we
 238 applied in the parallel empirical analysis, and have little influence on our testing. We
 239 therefore report only the results from the equations as described above.

240 2.2 | Empirical analyses

241 2.2.1 | Photosynthesis and respiration data

242 We combined two R_d datasets: the global respiration (GlobResp) and leaf carbon
243 exchange (LCE) datasets. GlobResp ([Atkin et al., 2015](#)) contains measurements of
244 leaf R_d , V_{cmax} , N_{area} and leaf mass per area (LMA) from 899 species at 100 locations
245 across the major biomes and continents, including data from an earlier compilation by
246 [Wright et al. \(2004\)](#). LCE ([Smith & Dukes, 2017a](#)) contains field measurements of
247 leaf carbon exchange and chemical traits from 98 species at 12 locations spanning 53°
248 latitude in North and Central America (Figure S1). Replicated measurements in LCE
249 on the same species and site were averaged. Juvenile samples were excluded. Leaf R_d
250 measurements in both datasets followed the same protocol. Both were taken on fully
251 expanded leaves in daytime after a period of dark adjustment. V_{cmax} values in
252 GlobResp were estimated by the ‘one-point method’ ([De Kauwe et al., 2016](#)) whereas
253 those in LCE were estimated from full $A-c_i$ curves. With a global dataset of $A-c_i$
254 curves (564 species from 46 field sites, covering a range of plant functional types), De
255 Kauwe et al. (2016) showed that ‘the one-point method’ can provide a robust
256 approach to expand the available set of field measurements on V_{cmax} . We present
257 analyses based on the combined datasets as the main results in this paper. However,
258 given that [Burnett et al. \(2019\)](#) recently showed that the one-point method may
259 underestimate V_{cmax} , we also analysed each dataset separately. The results are given in
260 the Supplementary Information.

261 We indexed T_g by the mean temperature during the thermal growing season with
262 temperatures above 0°C (mGDD₀) ([Harrison et al., 2010](#)). V_{cmax} and R_d values in both
263 datasets were provided with information about measurement leaf temperatures. V_{cmax}
264 and R_d values were adjusted both to mGDD₀ and to 25°C using the relevant
265 instantaneous responses, as given in Heskell et al. (2016) and Kattge and Knorr (2007),
266 respectively.

267 A global climatology of monthly temperature provided by the Climatic Research Unit
268 at a grid resolution of 10 arc minutes (CRU CL2.0) ([New et al., 2000](#)) was used to
269 provide estimates of mGDD₀ for each location. Thermal acclimation of R_d should in
270 principle apply to both C₃ and C₄ plants, but our theoretical prediction of V_{cmax}

271 acclimation here is developed for C_3 plants, and we did not include C_4 species in our
 272 analysis.

273 **2.2.2 | Statistical analysis**

274 The theoretical framework proposed here includes a series of quantitative predictions.
 275 Statistical analysis focused on testing the agreement between these theoretical
 276 predictions and data. To test our predictions of β_a and β_q quantitatively, the R_d and
 277 V_{cmax} data (assessed at mGDD_0 and 25°C) were first normalized with estimates of the
 278 site-mean PPFD absorbed by leaves (PPFD_L ; see Dong et al. (2017b)) before
 279 performing Ordinary Least Squares (OLS) regression against growth temperature.
 280 This normalization is appropriate because V_{cmax} is both predicted (equation 2) and
 281 observed (Niinemets & Keenan, 2012) to vary in proportion to PPFD. If it were
 282 omitted, the positive effect of PPFD on R_d and V_{cmax} would contribute to the fitted
 283 slope of mGDD_0 due to the correlation between those two variables (Figure S2).

284 PPFD_L was devised to deal with the fact that field-measured photosynthetic trait data
 285 reflect leaves developed at a range of irradiances at different levels in the canopy.
 286 PPFD_L is estimated from growing-season total incident PPFD at the top of the canopy
 287 (PPFD_0) as follows:

$$288 \text{PPFD}_L \approx f \text{PPFD}_0 / L \quad (8)$$

289 where f is the fraction of incident PPFD absorbed by the canopy (obtained from
 290 SeaWiFS data (Gobron et al., 2006)) and L is the leaf area index estimated from
 291 Beer's law:

$$292 L \approx - (1/k) \ln (1 - f) \quad (9)$$

293 with $k = 0.5$ (Dong et al., 2017a). PPFD_0 was calculated from CRU CL2.0 data using
 294 the SPLASH model (Davis et al., 2017).

295 We applied OLS linear regression of normalized and natural log-transformed R_d and
 296 V_{cmax} values against mGDD_0 using all-species and site-mean data, respectively. To
 297 check the impact of the PPFD normalization, we also performed regressions without
 298 it. We additionally applied mixed-effects models with species or sites contributing
 299 random effects. To test the uncertainty introduced by applying a single set of

300 instantaneous responses, whereas different kinetics responses might arise among
301 species and sites, we conducted a further OLS regression by using a subset of the
302 dataset when R_d and V_{cmax} were measured at a leaf temperature that differs from 25°C
303 or growth temperature less than 1°C.

304 To test the key assumption that $R_{d,25}$ is mainly determined by $V_{\text{cmax},25}$, we applied OLS
305 linear regression of R_d versus V_{cmax} (standardized to 25°C and separately to mGDD₀,
306 without transformation) to estimate b_{25} and b directly from the fitted slopes. We also
307 included LMA and soil pH as additional predictors in the regression described above.
308 LMA carries information on the structural component of plant leaves. Broadly
309 speaking, higher soil pH and cation exchange capability indicate higher soil fertility
310 (Jenny, 1994, Sinsabaugh & Follstad Shah, 2012), and pH has been shown to
311 influence χ (Wang et al., 2017b). These covariates were selected to test any potential
312 influences of leaf structure and soil nutrient availability on $R_{d,25}$. An estimate of soil
313 pH for each location was extracted from the Harmonized World Soil Database

314 (<http://www.iiasa.ac.at/web/home/research/researchPrograms/water/HWSD.html>).

315 Relationships of N_{area} with V_{cmax} and R_d were also tested by OLS linear regression
316 with or without LMA as an additional predictor. All regressions were performed in R
317 (version 3.5.1).

318 **3 | Results**

319 **3.1 | Testing the theoretical implications: thermal acclimation of R_d , V_{cmax} and** 320 **their ratio**

321 The predicted relationship of $V_{\text{cmax,tg}}$ to growth temperature (β_{aV}) was 5.5% K⁻¹ under
322 standard environmental conditions. The difference between the instantaneous
323 sensitivities of leaf R_d and V_{cmax} to temperature implies that the sensitivity of
324 acclimated $R_{d,tg}$ to temperature (β_{aR}) is 1.8% lower than that of $V_{\text{cmax,tg}}$ (β_{aV}), implying
325 a theoretical optimum rate of increase of $R_{d,tg}$ by 3.7% K⁻¹. Despite the various
326 simplifications we made, and large variation among species at any given site, these
327 theoretical values are very close to the data-fitted values – whether obtained from all-
328 species or site-mean analyses. They are however shallower than the 9.9% and 8.1%
329 K⁻¹ predicted for the instantaneous responses of V_{cmax} and R_d (Table 1, Figure 2). In
330 the all-species analysis, in spite of the large within-site spread, our theoretical

331 predictions are indistinguishable from the fitted regression coefficients of normalized
 332 and transformed $V_{\text{cmax,tg}}$ and $R_{\text{d,tg}}$ against mGDD_0 ($5.2 \pm 0.3\% \text{ K}^{-1}$, $R^2 = 0.48$ for
 333 $V_{\text{cmax,tg}}$, and $3.3 \pm 0.2\% \text{ K}^{-1}$, $R^2 = 0.34$ for $R_{\text{d,tg}}$) (Table 1, Figure 2). Growth
 334 temperature alone explains 45% and 65% of the observed site-mean variation in
 335 $V_{\text{cmax,tg}}$ and $R_{\text{d,tg}}$ respectively (Table S1, Figure S3).

336 Theoretically predicted values of the fractional sensitivities of acclimated $R_{\text{d},25}$ ($\beta_{\text{aR}25}$)
 337 and $V_{\text{cmax},25}$ ($\beta_{\text{aV}25}$) to temperature are negative ($-4.4\% \text{ K}^{-1}$) and this is consistent with
 338 the observed negative responses of $R_{\text{d},25}$ and $V_{\text{cmax},25}$ to temperature seen in the data
 339 (Table 1). The observed negative response of $V_{\text{cmax},25}$ to growth temperature is
 340 indistinguishable ($-4.2 \pm 0.3\% \text{ K}^{-1}$ for all-species, $-3.4 \pm 0.9\% \text{ K}^{-1}$ for site-mean)
 341 from our theoretical prediction, while the observed response of $R_{\text{d},25}$ is marginally
 342 larger than our all-species prediction ($-4.9 \pm 0.3\% \text{ K}^{-1}$), but indistinguishable in the
 343 site-mean analysis ($-4.3 \pm 0.7\% \text{ K}^{-1}$).

344 Regressions performed without PPFD-normalization showed temperature responses
 345 with the same signs (positive for V_{cmax} and R_{d} at growth temperature, negative at
 346 25°C) but slightly steeper (positive slopes) or shallower (negative slopes) than in the
 347 main analyses (Table S2) – as expected due to the confounding of PPF and
 348 temperature effects (Figure S2), which normalization removes. R^2 values were
 349 consistently greater in the main analyses, by 6-7% for V_{cmax} and R_{d} at growth
 350 temperature and 11-17% for V_{cmax} and R_{d} at 25°C .

351 Mixed-effects models show a similar acclimation pattern as the OLS regression
 352 models (Table S3). When the random effect from either species or site effect is
 353 included, the predicted positive (but weaker than instantaneous) thermal responses of
 354 $R_{\text{d,tg}}$ and $V_{\text{cmax,tg}}$ emerge from the data. The resulting negative thermal responses of
 355 $R_{\text{d},25}$ and $V_{\text{cmax},25}$ are also supported by the data. The data-fitted thermal sensitivities
 356 after acclimation show patterns in agreement with our theoretical predictions ($\beta_{\text{aR}} <$
 357 β_{aV} whereas $\beta_{\text{aR}25} = \beta_{\text{aV}25}$), although the fitted sensitivities in these analyses are
 358 marginally higher than the theoretical predictions (Table S3).

359 Using only a subset of the dataset with no temperature correction applied to the
 360 measured R_{d} and V_{cmax} , we again show thermal acclimation of $R_{\text{d},25}$ and $V_{\text{cmax},25}$
 361 consistent with our prediction. The responses of $R_{\text{d,gt}}$ and $V_{\text{cmax,gt}}$ to growth

362 temperature in this analysis are stronger than predicted, but the uncertainties are much
363 larger due to the limited size of this subset (Table S4).

364 Regressions based on the GlobResp and LCE datasets separately are generally
365 consistent with our theoretical predictions (Table S5). The LCE dataset shows a
366 stronger acclimation in $R_{d,tg}$ and a weaker acclimation in $R_{d,25}$ than V_{cmax} ($\beta_{aR} > \beta_{aV}$,
367 $\beta_{aR25} < \beta_{aV2}$), but the empirically estimated sensitivities are nevertheless close to our
368 theoretical predictions.

369 The prediction that b should decline with temperature by $1.8\% K^{-1}$ was consistent
370 with the fitted regressions of the ratio of $R_{d,tg}$ to $V_{cmax,tg}$; we observed a small but
371 significant negative response of b to growth temperature with a sensitivity of $2.0\% \pm$
372 0.3% , while b_{25} was indeed independent of $mGDD_0$ (Table 1, Table S3, Figure 2).
373 The fitted temperature response of $R_{d,tg}$ was consistently about 2% less steep than that
374 of $V_{cmax,tg}$ (Table 1). However, the observed temperature-dependence of this ratio is
375 weak and becomes non-significant in the analyses of site-mean data or the LCE
376 dataset alone (Table S1, S3, S5).

377 **3.2 | Testing the theoretical assumptions: relationships of dark respiration and** 378 **photosynthetic capacity to other variables**

379 We examined the relationships between R_d , V_{cmax} and other potential influences, in
380 order to further test our assumption that among those variables R_d is most strongly
381 correlated to variations in V_{cmax} . We found that measured R_d and V_{cmax} were positively
382 correlated in the datasets when normalized either to $mGDD_0$ ($R^2 = 0.25$) or to a
383 reference temperature of $25^\circ C$ ($R^2 = 0.16$) (Table S6). The canonical value of $b_{25} =$
384 0.015 in the photosynthesis model of [Collatz et al. \(1991\)](#), was similar to the fitted
385 value of $b_{25} = 0.014 \pm 0.001$ based on the regression of $R_{d,25}$ with respect to $V_{cmax,25}$
386 (Table S6). The inclusion of LMA or soil pH in addition to $mGDD_0$ as a predictor
387 provided negligible increases in explained variance (Table S7).

388 Relationships of leaf R_d and V_{cmax} to N_{area} were similar in strength when normalized to
389 $25^\circ C$ ($R^2 = 0.14$ and 0.12) (Table 2), but notably weaker when considered at growth
390 temperature ($R^2 = 0.05$ for $R_{d,tg}$ and 0.02 for $V_{cmax,tg}$). LMA and $V_{cmax,25}$ together
391 accounted for 42% variation in N_{area} , but most of this explanatory power comes from

392 LMA (Table 2). LMA and $R_{d,25}$ together explained 41% variation in N_{area} , but again
 393 most of this explanatory power is due to LMA (Table 2).

394 4 | Discussion

395 4.1 | Comparison with other studies

396 [Heskel et al. \(2016\)](#) provided an empirical function for leaf R_d at 25°C (equation (4) in
 397 Methods), where the parameter a (the logarithm of the basal rate of R_d at 0°C) is -1.60
 398 for tundra, declining to -2.75 for lowland tropical rainforest. We estimated a by
 399 rearranging equation (3) in Heskel et al. (2016) at a reference temperature of 25°C,
 400 and assuming proportionality between $R_{d,25}$ and $V_{\text{cmax},25}$, yielding independent
 401 estimates: $a = -1.41$ for tundra, and -2.50 for lowland tropical rainforest. The values
 402 of a given by [Heskel et al. \(2016\)](#) allow us to approximate the thermal sensitivity of a
 403 as $-4.6\% \text{ K}^{-1}$, assuming a growth temperature range of 25°C from tundra to rainforest:
 404 close to our prediction, $\beta_{\text{qR}} = -4.4\% \text{ K}^{-1}$. Our results are also consistent with previous
 405 findings showing that while $V_{\text{cmax,tg}}$ increases with growth temperature, $V_{\text{cmax},25}$, the
 406 amount of Rubisco, and the fraction of leaf N allocated to Rubisco all decline
 407 ([Scafaro et al., 2017](#)).

408 The canonical ratio $R_{d,25}/V_{\text{cmax},25} = 0.015$ ([Collatz et al., 1991](#)) perhaps co-incidentally
 409 lies within the 95% confidence intervals of the fitted slope (0.014 ± 0.001) obtained
 410 by regression of $R_{d,25}$ on $V_{\text{cmax},25}$ (Table S6). We found $R_{d,25}/V_{\text{cmax},25}$ was not
 411 significantly related to growth temperature but a small significant negative response
 412 of $R_{d,tg}/V_{\text{cmax,tg}}$ to growth temperature ($2.0\% \pm 0.3\% \text{ K}^{-1}$) (Figure 2). Our theory
 413 predicts a temperature dependence of the ratio of $R_{d,gt}$ to $V_{\text{cmax,gt}}$ due to their different
 414 instantaneous thermal responses, and this is observed, but the relationship to
 415 temperature is much less robust than that of R_d and V_{cmax} themselves.

416 4.2 | Implications of photosynthetic and respiratory acclimation

417 We predicted that field-measured $V_{\text{cmax,tg}}$ and $R_{d,tg}$ should increase with growth
 418 temperature by 5.5% and 3.7% per degree, respectively (Table 1, Figure 2). These
 419 responses are not instantaneous biochemical responses. They arise, instead, because
 420 of the differential temperature sensitivities of two quantities – the effective Michaelis-
 421 Menten coefficient of Rubisco (K) and the photorespiratory CO_2 compensation point

422 (Γ^*) (see equation 3 in Methods). The acclimated responses are determined by the
423 coordination between the Rubisco-limited and light-limited photosynthesis rates, and
424 achieved by the changes of the amount of Rubisco. These predicted thermal
425 sensitivities (β_{aV} , β_{aR}) are within the 95% confidence intervals of regression
426 coefficients independently derived from data (Table 1, Figure 2). The tundra site from
427 Alaska with growth temperature around 5°C is dominated by C₃ herbaceous and shrub
428 species, which show high $R_{d,tg}$ values comparable or even higher than the tropical
429 sites. Although the normalization by its low level of site-mean PPF_{D_L} contributes to
430 the high $R_{d,tg}$ values in Figure 2, the observed $R_{d,tg}$ values without normalization are
431 also higher than other sites with similar growth temperature (Figure S4). Meanwhile,
432 the observed $V_{cmax,tg}$ from this site seems quite comparable to other sites. This
433 decoupling might indicate some other energy consuming processes in leaves of those
434 species from extreme environmental conditions.

435 Many ecosystem and land-surface models disregard acclimation, and assume that the
436 long-term R_d and V_{cmax} responses to temperature follow the instantaneous functions
437 routinely observed ($\beta_{iV} = 9.9\% \text{ K}^{-1}$ ([Kattge & Knorr, 2007](#)) and $\beta_{iR} = 8.1\% \text{ K}^{-1}$
438 ([Heskel et al., 2016](#)). Our results contradict this assumption, and provide a
439 quantification of the temperature responses of both V_{cmax} and R_d that explicitly takes
440 acclimation into account. Given that V_{cmax} has been found to vary seasonally, and can
441 be predicted using the temperature of the previous week ([Smith & Dukes, 2018](#)), a
442 weekly to monthly acclimation time scale would be appropriate for LSMs to
443 incorporate this process. It has also been shown that high growth temperature has a
444 stronger negative impact on the instantaneous thermal response of V_{cmax} than that of
445 dark respiration ([Smith & Dukes, 2017b](#)). However, such effects occur above 30°C,
446 whereas the maximum growth temperature of the sampled sites we used here is only
447 ~28°C. More measures at hot sites would be helpful for future studies to understand
448 acclimation behaviour over a larger range of temperatures.

449 Theory also predicts that the amount of active Rubisco should decline with
450 temperature ($\beta_{qV} = -4.4\% \text{ K}^{-1}$), because the instantaneous response of V_{cmax} to
451 temperature is steeper than its acclimated response. At higher temperatures, less
452 active Rubisco is required to achieve the value of V_{cmax} indicated by the co-ordination
453 hypothesis (Figure 1). Lower levels of Rubisco require lower levels of maintenance
454 respiration for Rubisco turnover. Both predictions are quantitatively consistent with

455 observed negative responses of $R_{d,25}$ and $V_{cmax,25}$ to temperature (Table 1, Figure 2),
456 although the goodness of fit to the data at 25°C is weaker than that at growth
457 temperature.

458 The growth temperature-dependent trend in both V_{cmax} and leaf R_d emerges clearly
459 from the data despite considerable scatter around the regression (Figure 2). Much of
460 this scatter may be linked to within-site microclimatic variation (especially in PPFD)
461 that is not accounted for in analyses of this kind. Consistent with this hypothesis,
462 growth temperature explains a larger fraction of the variation in community-mean
463 values of V_{cmax} and R_d (Table S1) than in individual species values. The diversity
464 among species in other relevant traits and leaf life history may also explain some
465 within-site variation in V_{cmax} and R_d . For example, it has been shown that diverse
466 hydraulic strategies can influence plant photosynthetic capacity under the same
467 abiotic conditions ([Zhu et al., 2018](#)), while age-dependent leaf physiology can
468 significantly influence V_{cmax} and consequently the total canopy carbon uptake, e.g.
469 observed in tropical evergreen forests ([Albert et al., 2018](#)). Optimality-based theory
470 on respiration acclimation as presented here could (a) be applied globally at a
471 community-mean level, and (b) potentially be refined by explicitly considering
472 variations within the canopy in microclimate and differences among plant strategies
473 and leaf life histories.

474 Equation (3) could potentially allow predictions of the responses of leaf R_d to other
475 environmental determinants, including vapour pressure deficit, elevation and CO_2 .
476 Our theory predicts a downregulation of V_{cmax} and thus of R_d (both at 25°C and T_g) as
477 a response to increased atmospheric CO_2 . Consequently, enhanced thermal
478 acclimation in V_{cmax} and R_d ($\beta_{aV} = 2.7\% K^{-1}$ and $\beta_{aR} = 4.5\% K^{-1}$, $\beta_{qV} = \beta_{qR} = -5.4\%$
479 K^{-1}) are expected at high CO_2 . The data currently available do not allow us to test
480 these predictions, for various reasons including (a) the limited environmental range
481 covered by data, (b) correlations between potential explanatory variables and (c)
482 uncertainties in the measurement methods used in manipulative experiments
483 ([Ainsworth & Long, 2005](#)). Nevertheless, our theory provides testable predictions on
484 the acclimation of R_d to various environmental factors and also a simple, first-
485 principles approach to directly predict the thermal acclimation of R_d , which is one of

486 the most important mechanisms missing from current LSMs ([Huntingford et al.,](#)
487 [2017](#)).

488 **4.3 | On the correlation between R_d and N_{area}**

489 Empirical relationships of both $V_{\text{cmax},25}$ and $R_{d,25}$ to area-based leaf nitrogen content
490 (N_{area}) have been interpreted as showing ‘nitrogen limitation’ at the leaf level ([Luo et](#)
491 [al., 2004](#)) and form the basis of R_d prediction in some N-cycle enabled LSMs.
492 However, recent studies have shown two problems with this interpretation. First,
493 $V_{\text{cmax},25}$ accounts for only the metabolic component of N_{area} , whereas a large
494 component of variation in N_{area} is proportional to LMA ([Dong et al., 2017b](#), [Onoda et](#)
495 [al., 2017](#)). Here, we confirm that substantially more variation in N_{area} can be explained
496 by LMA than by V_{cmax} or R_d . This finding suggests that N_{area} is not the main
497 determinant of either V_{cmax} or R_d (Table 2). Second, global patterns of variation in
498 V_{cmax} have been shown to be predictable from climate alone ([Smith et al., 2019b](#)),
499 suggesting that $V_{\text{cmax},25}$ (and therefore $R_{d,25}$) is not determined by N_{area} , but rather
500 primarily by photosynthetic potential – which is set by the local climatic environment.
501 This potential in turn determines the metabolic component of N_{area} . Differences in soil
502 N availability then primarily influence plant-level carbon allocation, instead of leaf-
503 level N: the less soil N supply, the more carbon allocated belowground for N
504 acquisition ([LeBauer & Treseder, 2008](#), [Poorter et al., 2012](#)).

505 Our analysis therefore suggests an alternative to the common approach of carbon-
506 nitrogen cycle coupling applied in LSMs, whereby leaf nitrogen is prescribed by plant
507 functional types and used to predict V_{cmax} and leaf R_d at standard temperature, and
508 enzyme kinetics determines their temperature response at both fast (half-hourly) and
509 slower (weekly and longer) time scales. In our proposed approach, leaf nitrogen is
510 determined jointly by LMA (which may differ among plant functional types) and
511 V_{cmax} . V_{cmax} and R_d at standard temperature would then be considered independent of
512 plant functional type, but allowed to acclimate gradually to environmental conditions
513 following a simple optimality principle. Nitrogen availability would influence
514 primarily the allocation of nitrogen among plant organs, i.e. roots versus leaves.

515 **5 | Conclusion**

516 The theory developed here provides a first-principles approach to predicting the
517 thermal acclimation of leaf R_d , a key process missing from current LSMs. According
518 to both theory and data, the observed thermal acclimation of R_d follows the
519 optimization of V_{cmax} as predicted by the coordination hypothesis. This acclimation
520 dampens the instantaneous response of R_d to temperature and shows little influence
521 from other factors. The discrepancy between thermal acclimation and instantaneous
522 thermal response implies that both R_d and V_{cmax} , converted to 25°C or any other
523 arbitrarily chosen reference temperature, must decline with plant growth temperature.
524 These principles are straightforward to incorporate in an LSM framework. The theory
525 provides an explanation for observed correlations among N_{area} , V_{cmax} and R_d that
526 differs from the common assumption that N_{area} determines V_{cmax} and R_d , and supports
527 an alternative perspective on the coupling between terrestrial carbon and nitrogen
528 cycles.

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544 **Author contributions**

545 H.W. and I.C.P. derived the theory and designed the study. H.W. carried out all the
546 analyses and constructed the Figures and Tables, and wrote the first draft. All authors
547 contributed to the interpretation of the results and to the text.

548 **Data sharing and data accessibility**

549 The GlopResp database is accessible at the TRY plant trait database (www.try-db.org)
550 or by contacting Owen Atkin. The LCE dataset is publicly accessible at
551 <https://github.com/SmithEcophysLab/LCE/releases/tag/v1.1>. The climate data and
552 fractional absorbed photosynthetic active radiation data are publicly accessible from
553 Climatic Research Unit (<https://crudata.uea.ac.uk/cru/data/hrg/tmc/>), and NASA's
554 OceanColor Web (<https://oceancolor.gsfc.nasa.gov/data/seawifs/>), respectively.

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742

743 **Table**

744 **Table 1: Summary of Ordinary Least-Squares regressions for natural log-transformed**
 745 **leaf R_d and V_{cmax} , and their ratio as a function of growth temperature.** Both R_d and V_{cmax}
 746 have been converted to growth temperature ($R_{d,tg}$ and $V_{cmax,tg}$) and to 25°C ($R_{d,25}$ and $V_{cmax,25}$)
 747 from the measured leaf temperature, and normalized by site-mean leaf absorbed
 748 photosynthetic photon flux density. For comparison, the theoretical values of thermal
 749 sensitivities are shown together with the fitted coefficient and its confidence intervals. Non-
 750 significant coefficients are shown in grey.

Quantity	Theoretical value	Fitted coefficient	Confidence intervals		Intercept (mean ± se)	R^2	df
			2.5%	97.5%			
$R_{d,tg}$	0.037	0.033	0.029	0.038	-9.335±0.051	0.34	1245
$V_{cmax,tg}$	0.055	0.052	0.047	0.057	-6.255±0.054	0.48	1009
$R_{d,tg}/V_{cmax,tg}$	-0.018	-0.017	-0.023	-0.011	-3.044±0.061	0.03	1007
$R_{d,25}$	-0.044	-0.049	-0.054	-0.045	-7.261±0.052	0.25	1245
$V_{cmax,25}$	-0.044	-0.042	-0.047	-0.036	-3.922±0.054	0.25	1009
$R_{d,25}/V_{cmax,25}$	0	-0.007	-0.012	0.001	-3.302±0.060	0.00	1007

751

752 **Table 2: Summary statistics for Ordinary Least Squares regressions of leaf nitrogen**
 753 **content against leaf mass per area (LMA) and/or R_d or V_{cmax} .** R_d and V_{cmax} are assessed at
 754 growth temperature ($R_{d,\text{tg}}$ and $V_{\text{cmax,tg}}$), or 25°C ($R_{d,25}$ and $V_{\text{cmax},25}$). The fitted slopes are shown
 755 together with the intercept (mean \pm standard error), the adjusted coefficient of determination
 756 (R^2) and the degrees of freedom (df). All variables were natural-log transformed.

Coefficient					Intercept	R^2	df
$V_{\text{cmax,tg}}$	$V_{\text{cmax},25}$	$R_{d,\text{tg}}$	$R_{d,25}$	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

757 **Figure Legend**

758 **Figure 1: Schematic of the thermal sensitivities of leaf maximum carboxylation capacity**
759 **(V_{cmax}) and dark respiration (R_d).** Step 1: The “co-ordination hypothesis” predicts a positive
760 response of V_{cmax} to growth temperature (T_g). Due to increasing Rubisco oxygenation relative
761 to carboxylation, a higher V_{cmax} is required to achieve the optimal photosynthetic rate at
762 higher growth temperatures (T'_g). Step 2: When temperature increases, the value of V_{cmax}
763 achieved through the instantaneous response of Rubisco is super-optimal. Consequently, the
764 amount of Rubisco (indexed by V_{cmax} at the standard reference temperature of 25°C) must be
765 “down-regulated” from $V_{\text{cmax},25}$ to $V'_{\text{cmax},25}$. Step 3: We hypothesize that respiratory and
766 photosynthetic capacities are linked such that leaf $R'_{d,25}$ at growth temperature is a fixed
767 fraction of $V'_{\text{cmax},25}$. Step 4: Just as for V_{cmax} , leaf $R'_{d,25}$ at the new growth temperature is lower
768 than $R_{d,25}$ at the original growth temperature, implying an acclimated/adapted thermal
769 response that is less steep than the instantaneous response.

770 **Figure 2: Natural log-transformed leaf dark respiration (R_d), maximum carboxylation**
771 **capacity (V_{cmax}) and their ratio as a function of growth temperature (mGDD₀).** Both R_d
772 and V_{cmax} are standardized to growth temperature and to 25°C, and normalized by site-mean
773 leaf absorbed photosynthetic photon flux density. Solid blue lines are the fitted lines from
774 Ordinary Least Squares regressions. Solid black lines are theoretical predictions. Dashed lines
775 represent instantaneous temperature responses.

776



