

1 **Acclimation and adaptation components of the temperature dependence of plant**
2 **photosynthesis at the global scale**

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67

68 **Summary**

69 The temperature response of photosynthesis is one of the key factors determining
70 predicted responses to warming in global vegetation models (GVMs). The response may
71 vary geographically, due to genetic adaptation to climate, and temporally, due to
72 acclimation to changes in ambient temperature. Our goal was to develop a robust
73 quantitative global model representing acclimation and adaptation of photosynthetic
74 temperature responses.

75
76 We quantified and modelled key mechanisms responsible for photosynthetic temperature
77 acclimation and adaptation using a global dataset of photosynthetic CO₂ response curves
78 including data from 141 C₃ species from tropical rainforest to Arctic tundra. We separated
79 temperature acclimation and adaptation processes by considering seasonal and common-
80 garden datasets, respectively.

81
82 The observed global variation in the temperature optimum of photosynthesis was
83 primarily explained by biochemical limitations to photosynthesis, rather than stomatal
84 conductance or respiration. We found acclimation to growth temperature to be a stronger
85 driver of this variation, than adaptation to temperature at climate of origin.

86
87 We developed a summary model to represent photosynthetic temperature responses and
88 showed that it predicted the observed global variation in optimal temperatures with high
89 accuracy. This novel algorithm should enable improved prediction of the function of
90 global ecosystems in a warming climate.

91
92 **Key words:** Global vegetation models, climate of origin, growth temperature, V_{cmax} , J_{max} ,
93 maximum carboxylation capacity, maximum electron transport rate, AC_i curves

94 **Introduction**

95 The capacity of species to cope with increasing growth temperature is one of the key
96 determinants in range shifts and local extinction of species because their distribution and
97 range limits closely follow temperature isolines (Battisti *et al.*, 2005). Evidence suggests that
98 many species are adapted to their thermal environment of origin (Berry & Björkman, 1980)
99 but also exhibit the capacity to adjust to temporal variations in the temperature of their
100 environment (Rehfeldt *et al.*, 2001; Valladares *et al.*, 2014). However, the mechanisms that
101 determine these responses are not well understood, making it challenging to predict the fate
102 of plants in a changing climate.

103 Global vegetation models (GVMs) are one of the principal tools used to predict future
104 terrestrial vegetation carbon balance (Rogers *et al.*, 2017a; Mercado *et al.*, 2018). The
105 temperature response of leaf-scale net photosynthesis (referred to as A_n -T response hereafter)
106 is one of the key processes in these models. The effect of warming on modelled
107 photosynthesis depends on the A_n -T response function used in the model, and in particular,
108 the optimum temperature of photosynthesis (T_{optA}) (Booth *et al.*, 2012). Decades of
109 empirical studies have shown that the A_n -T responses of plants vary geographically,
110 suggesting genetic adaptation of species to their climate of origin (Fryer & Ledig, 1972;
111 Slatyer, 1977; Slatyer, 1978; Berry & Björkman, 1980; Gunderson *et al.*, 2009). Considerable
112 evidence also shows that plants have the capacity to adjust the A_n -T response following
113 temporal changes in ambient temperature, a response known as thermal acclimation (Way &
114 Sage, 2008; Hall *et al.*, 2013; Way & Yamori, 2014; Yamaguchi *et al.*, 2016; Way *et al.*,
115 2017). In a recent review, Yamori *et al.* (2014) reported inherent differences in the A_n -T
116 response and its acclimation capacity among photosynthetic pathways (C_3 , C_4 and CAM) and
117 functional types (annual vs perennial, deciduous vs evergreen) that often differ in their
118 climatic distributions. However, the current representations of A_n -T response in GVMs do not
119 capture this empirical knowledge well (Smith & Dukes, 2013; Lombardozzi *et al.*, 2015;
120 Smith *et al.*, 2016; Mercado *et al.*, 2018). Most GVMs use either a single A_n -T response
121 function for all species or represent broad geographical variation in the A_n -T response by
122 using plant functional type(s) (PFTs)-specific functions without considering thermal
123 acclimation. Robust representation of adaptation and acclimation of A_n -T response in GVMs
124 is challenging as we lack a quantitative assessment of acclimation and adaptation of
125 photosynthetic temperature responses on a global scale (Stinziano *et al.*, 2017).

126 Many GVMs incorporate the biochemical model of C₃ photosynthesis (Farquhar *et*
127 *al.*, 1980; Rogers *et al.*, 2017a ; referred to as FvCB hereafter). Therefore it is both tractable
128 and valuable to encapsulate the mechanisms of photosynthetic temperature adaptation and
129 acclimation in terms of parameters of the Farquhar model (Hikosaka *et al.*, 1999; Dreyer *et*
130 *al.*, 2001; Medlyn *et al.*, 2002b; Dillaway & Kruger, 2010). The model has two key
131 parameters, for which the temperature response is particularly important; the maximum rate
132 of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) activity (V_{cmax}) and the
133 maximum potential electron transport rate (J_{max}) (Farquhar *et al.*, 1980). GVMs use two basic
134 functional forms to characterize the instantaneous temperature response of the key FvCB
135 model parameters, namely the standard and peaked Arrhenius functions (Medlyn *et al.*,
136 2002a). Most empirical studies of the instantaneous temperature response of V_{cmax} and J_{max}
137 have used the peaked Arrhenius model, which has four key parameters; the basal rate of
138 either V_{cmax} or J_{max} at a standard temperature of 25°C (V_{cmax25} or J_{max25}), the activation energy
139 (E_a), the de-activation energy (H_d), and the entropy term (ΔS). The peaked Arrhenius model
140 can also be used to calculate the optimum temperatures of V_{cmax} ($Topt_V$) and J_{max} ($Topt_J$).
141 These parameters have now been documented for a wide range of species from different
142 biomes and PFTs (Onoda *et al.*, 2005; Rogers *et al.*, 2017b; Slot & Winter, 2017). Evidence
143 suggests that the Arrhenius model parameters vary significantly across plant taxa but also that
144 these parameters have the capacity to acclimate to the growth temperature (Crous *et al.*, 2013;
145 Crous *et al.*, 2018).

146 Several meta-analytic studies have attempted to characterise species variation in the
147 model parameters. Medlyn *et al.* (2002a) compared the temperature response of key FvCB
148 model parameters across different species but reported a poor relationship overall between
149 the optimum temperature for photosynthesis and the temperature of the growing environment.
150 They reported lower $Topt_V$ and $Topt_J$ for plants grown in boreal compared to temperate
151 climates, but it was unclear whether this difference was due to inherent genetic differences
152 among the boreal and temperate species, or acclimation to prevailing growth temperature. In
153 an analysis of 23 species, (Hikosaka *et al.*, 2006) identified two important mechanisms of
154 photosynthetic temperature acclimation, namely E_a of V_{cmax} (E_{aV}) and J_{max} (E_{aJ}) and the ratio
155 of $J_{max} : V_{cmax}$ (JV_r). The most comprehensive synthesis to date of the biochemically-based
156 plant photosynthetic temperature response is that of Kattge and Knorr (2007), who compared
157 the instantaneous temperature response of V_{cmax} and J_{max} across 36 species. This study found
158 a lack of thermal acclimation of E_{aV} and E_{aJ} but reported significant acclimation

159 relationships for JV_r and ΔS of V_{cmax} (ΔS_V) and J_{max} (ΔS_J). Importantly, Kattge and Knorr
160 (2007) synthesised these relationships into a simple and generalizable form that enabled
161 direct implementation into GVMs, thus providing a means to quantify the effect of thermal
162 acclimation of photosynthesis on terrestrial carbon cycle predictions (Chen & Zhuang, 2013;
163 Lombardozzi *et al.*, 2015; Smith *et al.*, 2016) as well as on biophysical consequences in
164 future climates (Smith *et al.*, 2017).

165 Despite the success of the Kattge and Knorr (2007) algorithms, the functions have
166 several limitations. Firstly, the parameterization process did not consider potential inter-
167 specific differences in photosynthetic temperature response; all changes were attributed to
168 differences in growth temperature. Hence, the response incorporates elements of both
169 temperature adaptation and acclimation without resolving the extent of the contribution of the
170 two processes. Given that acclimation can occur over days and adaptation takes many
171 generations, the importance of resolving the relative contribution of the two processes is
172 critical. Recently, Mercado *et al.*, (2018) showed that assuming the relationships represent
173 both adaptation and acclimation, or adaptation only, leads to significantly different
174 conclusions about the trajectory of future terrestrial carbon storage under warming. Their
175 results further highlight the importance of separating photosynthetic thermal adaptation and
176 acclimation when simulating current and future carbon storage. However, to date, few studies
177 have separated species differences in temperature adaptation from temperature acclimation
178 processes (Lin *et al.*, 2013).

179 Secondly, the data used to derive the Kattge and Knorr (2007) functions came mainly
180 from northern temperate and boreal trees and lacked globally important PFTs such as tropical
181 forests and Arctic tundra. As a result, the growth temperature range only varied from 11 to
182 29°C (Kattge and Knorr 2007), which is substantially narrower than growth temperatures
183 simulated in GVMs. Therefore, the analysis of Kattge and Knorr (2007) could be improved
184 with a broader global dataset directly addressing the relative roles of temperature acclimation
185 and adaptation.

186 Thirdly, the ability of the acclimation functions to capture the observed differences in
187 temperature optima of light saturated net photosynthesis ($Topt_A$) has not been directly tested.
188 It is not clear whether making adjustments to $Topt_V$ and $Topt_J$ improves the ability of models
189 to capture changes in $Topt_A$; some studies have reported similar $Topt_A$ values even with
190 significantly different $Topt_J$ among species (Vårhammar *et al.*, 2015). Moreover, the
191 photosynthetic temperature response is controlled not only by the photosynthetic

192 biochemistry, but also by stomatal and respiratory processes. Sensitivity analysis suggests
193 that all three component processes are equally important in determining the T_{opt_A} at leaf
194 scale (Lin *et al.*, 2012) as well as at canopy scale (Tan *et al.*, 2017) but none of the previous
195 review studies addressed how the latter two components affected T_{opt_A} .

196 Given the need for robust representation of photosynthetic temperature acclimation
197 and adaptation in GVMs, and its importance in predicting future global carbon budget
198 (Lombardozzi *et al.*, 2015, Smith *et al.*, 2016, Mercado *et al.*, 2018) and climate (Smith *et al.*,
199 2017), we quantified and modelled the mechanisms that underlie the observed differences in
200 T_{opt_A} among species and growth temperatures. We hypothesized that T_{opt_A} would be
201 strongly driven by adaptation to the climate of origin, while temperature acclimation would
202 further modify the temperature optimum in response to seasonal changes in temperature of
203 the growth environment. To test these hypotheses, we compiled a global database of
204 photosynthetic CO₂ response curves measured at multiple leaf temperatures to simultaneously
205 resolve the temperature optima of A_{net} , V_{cmax} and J_{max} . The data comprised a total of 141
206 species from tropical rainforests to Arctic tundra. Included in this database were datasets: (i)
207 from common-garden studies, which were used to quantify effects of adaptation alone on
208 T_{opt_A} ; and (ii) comprising time course studies that measured plants under contrasting
209 prevailing ambient temperatures, which are used to quantify effects of temperature
210 acclimation alone. We combined the identified effects of climate adaptation and temperature
211 acclimation to derive a general global model of temperature responses that is then tested
212 against (iii) a third, independent, biogeographic dataset measured on mature plants growing
213 in their native environments across the globe.

214

215 **Materials and methods**

216 *Data sources*

217 We compiled a global database of datasets consisting of leaf photosynthetic CO₂
218 response measurements (referred to as ACi curves hereafter) measured at multiple leaf
219 temperatures and saturating irradiance levels. The database covers 141 species from 38
220 experiments conducted around the world (Fig. S1, Table S1). Site latitude ranged from 42°48'
221 S to 71°16' N and mean annual growing season temperature (long-term average temperature
222 of months where mean monthly temperature is above 0°C) ranged from 3 to 30°C.

223 The method of data collection was consistent across all datasets. In most datasets,
224 measurements were started at ambient CO₂ levels (360-400 ppm; depending on the year of
225 data collection) and changed stepwise through a series of subambient (40-400 ppm) to
226 superambient saturating CO₂ concentrations (400-2000 ppm). The same measurement
227 protocol was repeated on the same leaf at different leaf temperatures. Measurements were
228 made at saturating irradiance (Table S1) using a portable photosynthesis system with standard
229 leaf chambers, in most cases the Licor 6400 (Licor Biosciences, Lincoln, NE, USA) although
230 some measurements were made with the Walz-CMS system (Walz, Effeltrich, Germany). We
231 visually inspected every ACi curve in the dataset for possible outliers and erroneous data
232 points (i.e. negative intercellular CO₂ concentrations). We used criteria based on De Kauwe
233 *et al.* (2016) to screen individual ACi curves for the analysis performed in this paper. Curves
234 were excluded from the analysis if the fitted function (see below) had a $r^2 < 0.99$ (however, if
235 the number of replicates available for a given occasion was limited, the threshold r^2 was
236 reduced to 0.90; ~9% of the total ACi curves included in the analysis). After screening, the
237 dataset contained a total of 3498 ACi curves measured at leaf temperatures ranging from 1 to
238 50°C.

239

240 *Estimating temperature optimum for leaf net photosynthesis ($T_{opt,A}$)*

241 Ambient leaf net photosynthesis (A_{net}) at each temperature was obtained from either the
242 initial direct measurements at ambient CO₂ concentrations or extracted from the ACi curves.
243 For curves where the first point was not measured at ambient CO₂ level, we extracted the A_{net}
244 value at the measured sample CO₂ concentration falling between 300 and 400 ppm. We
245 estimated the temperature optimum for A_{net} , $T_{opt,A}$, by fitting a widely used model of
246 instantaneous photosynthetic temperature response (Gunderson *et al.*, 2009; Crous *et al.*,

247 2013; Sendall *et al.*, 2015; Vårhammar *et al.*, 2015) (Eqn 1) to the net photosynthesis
 248 measurements. The model is a quadratic equation, expressed as:

$$249 \quad A_{net} = A_{opt} - b(T - T_{opt_A})^2 \quad \text{Eqn 1}$$

250 where A_{net} is the net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at a given leaf temperature, T ($^{\circ}\text{C}$),
 251 T_{opt_A} is the temperature optimum for photosynthesis ($^{\circ}\text{C}$) A_{opt} is the net photosynthetic rate at
 252 T_{opt_A} , and the parameter b (unitless) describes the degree of curvature of the relationship.

253

254 *Parameterising biochemical component processes of photosynthesis*

255 We used the FvCB model to characterize photosynthetic biochemical component
 256 processes. The model represents leaf net photosynthesis rate as the minimum of three rates;
 257 the Rubisco carboxylation limited photosynthetic rate (W_c), the RuBP-regeneration limited
 258 photosynthetic rate (W_j), and the triose phosphate utilization limited rate (W_p). The widely
 259 used formulation and parameterization of the FvCB model is of the form (Eqn 2-6).

$$260 \quad A_{net} = \min(W_c, W_j, W_p) \left(1 - \frac{\Gamma^*}{C_i}\right) - R_L \quad \text{Eqn 2}$$

$$261 \quad W_c = V_{cmax} \frac{C_i}{C_i + K_c \left(1 + \frac{O_i}{K_o}\right)} \quad \text{Eqn 3}$$

$$262 \quad W_j = \frac{J}{4} \frac{C_i}{(C_i + 2\Gamma^*)} \quad \text{Eqn 4}$$

$$263 \quad W_p = 3 TPU \quad \text{Eqn 5}$$

264

265 where V_{cmax} is the maximum rate of ribulose-1,5-bisphosphate carboxylase-oxygenase
 266 (Rubisco) activity, C_i and O_i ($\mu\text{mol mol}^{-1}$) are intercellular CO_2 and O_2 concentrations
 267 respectively, K_c and K_o ($\mu\text{mol mol}^{-1}$) are Michaelis–Menten coefficients of Rubisco activity
 268 for CO_2 and O_2 respectively, Γ^* ($\mu\text{mol mol}^{-1}$) is the CO_2 compensation point in the absence of
 269 photorespiration, TPU ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the rate of triose phosphate export from the
 270 chloroplast, R_L ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the non-photorespiratory CO_2 evolution in the light, and J
 271 ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the rate of electron transport at a given light level. J is related to incident
 272 photosynthetically active photon flux density (Q , $\mu\text{mol m}^{-2} \text{s}^{-1}$) by

273

$$274 \quad \theta J^2 - (\alpha Q + J_{max})J + \alpha Q J_{max} = 0 \quad \text{Eqn 6}$$

275

276 where J_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the potential rate of electron transport, α ($\mu\text{mol mol}^{-1}$) is the
 277 quantum yield of electron transport, and θ (dimensionless) is the curvature of the light
 278 response curve (Farquhar *et al.*, 1980; Medlyn *et al.*, 2002a; Medlyn *et al.*, 2002b; Kattge &
 279 Knorr, 2007; Sharkey *et al.*, 2007).

280 We parameterized Eqns 3 – 6 using the *fitacis* function within the *plantecophys*
 281 package (Duursma, 2015) in R version 3.3.2 (R Development Core Team, 2012). We
 282 assumed the Bernacchi *et al.* (2001) kinetic constants for the temperature response of K_c , K_o
 283 and Γ^* as given in Medlyn *et al.* (2002a). We used measurement Q in Eqn 6 whenever
 284 available (see Table S1); otherwise we assumed a fixed value of $1800 \mu\text{mol m}^{-2}\text{s}^{-1}$. We
 285 assumed constant values of α ($0.24 \mu\text{mol mol}^{-1}$) and θ (0.85; unitless) for all datasets (Medlyn
 286 *et al.*, 2007); these parameter values have a relatively minor effect on the magnitude of
 287 estimated J_{\max} (Medlyn *et al.*, 2002a). The estimated parameters, $V_{c\max}$ and J_{\max} , are apparent
 288 values as we assumed infinite mesophyll conductance (g_m). The significance of g_m for $V_{c\max}$
 289 and J_{\max} estimates and their temperature response has been discussed elsewhere (Crous *et al.*,
 290 2013; Bahar *et al.*, 2018). Here, there are insufficient data to quantify g_m and hence it would
 291 have been inappropriate to include in our analysis (see Rogers *et al.*, 2017a).

292 We tested two ACi curve fitting routines; one with and one without TPU limitation
 293 (Eqn 5). Accounting for TPU limitation in the FvCB model did not affect the estimated
 294 photosynthetic capacities, apparent $V_{c\max}$ and J_{\max} (Fig. S2) suggesting that at ambient CO_2
 295 levels, net photosynthesis was rarely limited by TPU (results not shown). Hence, we focused
 296 on the temperature responses of apparent $V_{c\max}$ and J_{\max} as the principal biochemical
 297 components affecting the T_{optA} .

298 The temperature responses of $V_{c\max}$ and J_{\max} were fitted using the peaked Arrhenius
 299 function:

$$300 \quad k_{T_k} = k_{25} \exp \left[\frac{E_a(T_k - 298.15)}{(298.15 R T_k)} \right] \frac{1 + \exp\left(\frac{298.15 \Delta S - H_d}{298.15 R}\right)}{1 + \exp\left(\frac{T_k \Delta S + H_d}{T_k R}\right)} \quad \text{Eqn 7}$$

301 where k_{T_k} is the process rate (i.e. $V_{c\max}$ or J_{\max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) at a given temperature, T_k (K), k_{25}
 302 is the process rate at $25 \text{ }^\circ\text{C}$, R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$), and E_a (kJ mol^{-1})
 303 is the activation energy term that describes the exponential increase in enzyme activity with
 304 the increase in temperature, H_d (kJ mol^{-1}) is the deactivation energy term that describes the
 305 decline in enzyme activity at higher temperature due to denaturation of enzymes, and ΔS (J
 306 $\text{mol}^{-1} \text{ K}^{-1}$) is the entropy term which characterize the changes in reaction rate caused by

307 substrate concentration (Liang *et al.*, 2018). To avoid over-parameterization, we assumed a
308 fixed value of 200000 J mol⁻¹ for H_d in Eqn 7 for all species (Dreyer *et al.*, 2001; Medlyn *et*
309 *al.*, 2002a).

310 The optimum temperature for k_{Tk} is given by:

$$311 \quad T_{opt} = \frac{H_d}{\Delta S - R \ln\left(\frac{E_a}{H_d - E_a}\right)} \quad \text{Eqn 8}$$

312

313 *Assessing the contribution of stomatal and respiratory processes*

314 The optimum temperature for photosynthesis is determined by stomatal and respiratory
315 processes as well as biochemical processes (Medlyn *et al.*, 2002a; Lin *et al.*, 2012). Stomatal
316 conductance values are potentially affected by the measurement protocol used in ACi curve
317 measurements which rarely replicates the ambient conditions. Therefore, to assess the relative
318 contribution of stomatal processes to T_{optA} , we calculated the net photosynthesis rate at a
319 fixed C_i of 275 $\mu\text{mol mol}^{-1}$ from each ACi curve, interpolating the curve using the FvCB
320 model with parameters fitted to that curve. A fixed C_i of 275 $\mu\text{mol mol}^{-1}$ was chosen as it
321 roughly corresponds to 70% of ambient $[\text{CO}_2]$. When the photosynthetic rate is scaled to a
322 common C_i , it eliminates the effect of variation in stomatal conductance on photosynthesis,
323 isolating the temperature effects on photosynthetic biochemistry. Similar to net
324 photosynthesis, the temperature optimum for photosynthesis at a fixed C_i ($T_{optA275}$) was
325 estimated for each species by fitting Eqn 1. We compared $T_{optA275}$ with T_{optA} to estimate the
326 effect of variation in stomatal conductance on the temperature optimum for photosynthesis.

327 We fitted standard Arrhenius function (Eqn 9) to R_L values obtained from ACi curves
328 to assess the effect of respiratory component processes on T_{optA} . We estimated two
329 parameters R_{L25} (R_L at 25°C) and activation energy of R_L (E_a). Similar to J_{max} and V_{cmax} , linear
330 regression was used to test for temperature adaptation and acclimation of R_L .

$$331 \quad R_L = R_{L25} \exp\left(\frac{E_a(T_k - 298.15)}{298.15 R T_k}\right) \quad \text{Eqn 9}$$

332 where, R_{L25} is the rate of respiration in light at 25°C

333

334 *Test for local adaptation and seasonal temperature acclimation of T_{optA}*

335 We divided the database into three subsets: (i) mature plants growing in their native
336 environments; (ii) common-garden datasets; and (iii) datasets with seasonal photosynthetic
337 measurements. We used a subset of the data collected in mature plants (i) to identify the
338 patterns in photosynthetic temperature responses of plants in native environments and for
339 model evaluation. Temperature responses in this subset include the effects of both adaptation
340 to the native environment, and acclimation to the prevailing temperature. We used the
341 common garden (ii) and seasonal measurements (iii) subsets to estimate the relative
342 contributions of adaptation and acclimation, respectively, in determining the observed trends
343 with temperature for plants in native environments

344 For plants growing in native environments, we derived relationships between photosynthetic
345 parameters and the prevailing temperature of the growing environment defined as the mean
346 air temperature for the 30 days prior to gas exchange measurements (Kattge & Knorr, 2007)
347 (T_{growth}), to identify the temporal trends in photosynthetic temperature responses. We derived
348 T_{growth} using on-site measured real time daily air temperature for most of the datasets, but for
349 three datasets (Hinoki cypress, Japan; Mongolian oak, Japan; and Scots pine, Finland; Table
350 S1), we extracted T_{growth} values from the original publications as on-site temperature
351 measurements were not available. We used a general linear model to parameterise the
352 observed responses in mature plants dataset (Eqn 10)

353

$$354 \quad f(T_{growth}) = a + bT_{growth} \quad \text{Eqn 10}$$

355 where a and b are the intercept and slope respectively.

356 Seasonal datasets provide the opportunity to test the acclimation capacity of different
357 species to temporal changes in the ambient temperature of the growing environment. Here,
358 we correlated photosynthetic parameters with growth temperature, T_{growth} , defined as the mean
359 air temperature for the 30 days prior to gas exchange measurements. Similar to the mature
360 plants dataset, we derived T_{growth} using on-site measured daily air temperature for most of the
361 datasets. For datasets where real-time meteorological data were not available, we extracted
362 T_{growth} values from the original publications.

363 Common gardens provide an opportunity to test for adaptation, as species with
364 different climates of origin are grown at a common growth temperature. The common garden
365 datasets included field trials and experiments in controlled environmental conditions which
366 included two or more species or provenances with contrasting climates of origin. We located
367 the seed source of each species or provenance (latitude and longitude) using published

368 information (Table S1). We used 30" resolution WorldClim climatology data (WorldClim
 369 1.4;(Hijmans *et al.*, 2005)) to estimate long-term average (1960-1990) air temperature at seed
 370 source. With reference to the species selection criteria used in several common garden
 371 studies (Lin *et al.*, 2013; Vårhammar *et al.*, 2015), we defined mean maximum air
 372 temperature of the warmest month at species' seed source as the species' home temperature
 373 (T_{home}) and derived relationships between photosynthetic parameters and T_{home} to test for
 374 adaptation of species' A_n -T response to climate of origin. We repeated the same analysis with
 375 two other forms of species' home temperature, 1. mean growing season air temperature and
 376 2. mean temperature of the warmest quarter, to test whether our results were altered
 377 depending on the definition of climate of origin.

378 For both common garden and seasonal subsets, we used linear regression against T_{home}
 379 and T_{growth} (Eqns 11, 12) to test for temperature adaptation and acclimation, respectively, of
 380 T_{optA} , $T_{optA275}$, the photosynthetic biochemical parameters (V_{cmax} , and J_{max}), and their
 381 temperature response parameters (see Eqns 7 and 8). To test the effect of different
 382 biochemical parameters on temperature optimum for photosynthesis, we used linear
 383 regression between $T_{optA275}$ and temperature response parameters of V_{cmax} and J_{max} .

384

385 *Representing acclimation and adaptation in vegetation models*

386 We derived functions to represent photosynthetic temperature acclimation and adaptation in
 387 GVMs. If a given parameter showed only acclimation to growth temperature, the function
 388 used was:

$$389 \quad f(T_{growth}) = A_{ac} + \alpha_{ac}T_{growth} \quad \text{Eqn 11}$$

390 where, A_{ac} is the parameter value when $T_{growth}=0$ and α_{ac} is the acclimation coefficient ($^{\circ}\text{C}^{-1}$)

391

392 If a parameter showed only adaptation to climate of origin, the function was:

$$393 \quad f(T_{home}) = A_{ad} + \alpha_{ad}T_{home} \quad \text{Eqn 12}$$

394

395 We combined Eqns 11 and 12 to represent both acclimation and adaptation, defined as

396

$$397 \quad f(T_{home}, T_{growth}) = A_{ad} + \alpha_{ad}T_{home} + \delta_{ac}(T_{growth} - T_{home}) \quad \text{Eqn 13}$$

398

399 here, δ_{ac} is the acclimation coefficient corresponding to a unit deviation in T_{growth} from the
400 species' T_{home} ($^{\circ}\text{C}^{-1}$). We parameterised Eqn 11 and 12 independently using data from
401 seasonal photosynthetic response studies (Eqn 11) and common garden experiments (Eqn
402 12). Eqn 13 was parameterised using combined seasonal and common garden datasets. We
403 implemented the modified functions into the FvCB model (see Duursma, 2015) to simulate
404 photosynthetic temperature response curves at a constant C_i of $275 \mu\text{mol mol}^{-1}$ and tested
405 how well the leaf scale photosynthesis model captured the observed temperature optimum of
406 photosynthesis in the mature plants dataset. This provided an independent comparison as the
407 mature plants dataset was not used to parameterise the temperature acclimation and
408 adaptation functions (Eqn 11-13).

409

410 *Statistical analysis*

411 Parameters of Eqn 1, 7-9 were estimated in a non-linear mixed model framework (Zuur *et al.*,
412 2009) using the *nlme* function within the *nlme* package in R version 3.3.2 (R Development
413 Core Team, 2012). Replicate trees and/or leaves of the same species were included as
414 random effects in model. However, when datasets contained measurements of multiple
415 species (e.g. Brazilian rainforests, Australian rainforests and Australian semi-arid woodland
416 datasets, Table S1), individual species were considered as a random variable in the model.
417 Similarly, Eqns 11-13 were parameterized in a linear mixed model framework using the
418 inverse of the standard error (SE) of each parameter of Eqn 1, 7-9 as the weighting scale to
419 account for parameter uncertainty (Zuur *et al.*, 2009; Lin *et al.*, 2015). We tested whether the
420 model parameters (Eqn 11-13) significantly differed among datasets (and/or species) by
421 fitting linear mixed models with and without random slopes and intercepts for each dataset
422 (and or species). These models were then compared using a likelihood ratio test (Zuur *et al.*,
423 2009) to determine whether the acclimation and adaptation coefficients differed among
424 species. We used standard model validation tools (normal quantile plots and residual plots) to
425 test the underlying assumptions in linear mixed models and used marginal and conditional r^2
426 values to evaluate the goodness of fit (Nakagawa & Schielzeth, 2013). The complete database
427 used for this analysis will be available as a public data product through (*link provided after*
428 *acceptance*). The code used for the entire analysis is publicly available through
429 <https://bitbucket.org/Kumarathunge/photom>

430

431 **Results**

432 *Temperature optimum for net photosynthesis at saturating irradiance (T_{opt_A})*

433 The temperature optimum for leaf level net photosynthesis at saturating irradiance (T_{opt_A}) of
434 mature plants in their natural habitats was strongly correlated with the temperature of the
435 growth environment (T_{growth} ; mean air temperature of preceding 30 days) (Fig. 1a, Table 1).
436 Values of T_{opt_A} ranged from 16.3 to 32.4 °C, where the minimum and maximum values were
437 observed for Arctic vegetation and tropical evergreen trees, respectively. The rate of increase
438 in T_{opt_A} was 0.62 ± 0.07 °C per °C increase in T_{growth} .

439 In the seasonal dataset (Fig. 1b), we found strong evidence for acclimation of T_{opt_A} to
440 the prevailing growth temperature. T_{opt_A} showed a significant increasing trend with T_{growth} .
441 The mean rate of increase in T_{opt_A} was 0.34 ± 0.05 °C per unit increase in T_{growth} (Table 1).
442 In contrast, no trend was observed with climate of origin in common garden studies (Table
443 1). Here, we tested for a relationship between T_{opt_A} and the T_{home} (1960-1990 mean
444 maximum air temperature of the warmest month at species' seed source) and we did not find
445 any significant relationship for T_{opt_A} with T_{home} . (Fig. 1c, Table 1). The results were similar
446 for the two alternative definitions of the climate of origin (Table S2). The lack of a significant
447 relationship with the species' home temperature in the common garden datasets suggests that
448 the variation in T_{opt_A} of mature plants across ecosystems (Fig. 1a) is more strongly driven by
449 acclimation to growth temperatures (Fig. 1b) than by local adaptation to climate of origin
450 (Fig. 1c).

451

452 *Temperature optimum for photosynthesis at a common C_i ($T_{opt_{A275}}$)*

453 Similar to T_{opt_A} , $T_{opt_{A275}}$ showed a strong correlation with T_{growth} in mature plants
454 across ecosystems (Fig. 1d, Table 1). We found no significant differences in either intercept
455 or slope of the linear regression between T_{opt_A} and $T_{opt_{A275}}$ vs T_{growth} (Table 1), in both the
456 mature (Fig 1a, d) and seasonal (Fig 1b, e) datasets, strongly suggesting that the observed
457 variation in T_{opt_A} among ecosystems is not due to variation in the stomatal limitation of
458 T_{opt_A} . This result also suggests that the observed seasonal pattern of T_{opt_A} (Fig. 1b) was not
459 driven by stomatal processes but rather by the effects of photosynthetic biochemical
460 processes. Similar to T_{opt_A} , species in common garden studies did not show significant trends
461 for $T_{opt_{A275}}$ with T_{home} (Fig. 1f).

462

463 *Temperature dependence of biochemical capacities, J_{max} & V_{cmax}*

464 Similar to $Topt_A$, we found a strong increase in both $Topt_V$ and $Topt_J$ with T_{growth} in the
465 mature plants dataset (Fig. 2a,d). The slopes of the linear regression with T_{growth} were similar
466 for $Topt_V$ and $Topt_J$ (0.71 ± 0.20 and $0.63 \pm 0.15^\circ\text{C}^\circ\text{C}^{-1}$ respectively). These sensitivities are
467 similar in magnitude to the sensitivity of $Topt_A$ and $Topt_{A275}$ to T_{growth} in the mature plants
468 dataset. For V_{cmax} , the trend in $Topt$ was caused by an increase ($p \approx 0.06$) in Ea_V with increasing
469 T_{growth} , and a strong decline in ΔS_V (Fig. 2b,c). For J_{max} , however, there was no change in Ea_J ,
470 only a decline in ΔS_J with increasing T_{growth} (Fig. 2e,f).

471 We deconstructed the observed trends across biomes shown in Fig. 2 by looking at
472 seasonal datasets (Fig. 3) and common garden studies (Fig. 4) independently to identify the
473 effect of seasonal acclimation and local adaptation of photosynthetic biochemical component
474 processes. We found a strong increase in $Topt_V$ and $Topt_J$ with T_{growth} (Fig. 3a,d). The rate of
475 increase in $Topt_J$ per unit increase in T_{growth} was slightly higher than the $Topt_V$ (Table 1) but
476 the difference was not significant. Further, these sensitivities were found to be similar to the
477 sensitivity of both $Topt_A$ and $Topt_{A275}$ to T_{growth} . Similar to the mature plants dataset, we found
478 a significant positive trend for Ea_V and a decreasing trend ($p \approx 0.08$) for ΔS_V with increasing
479 T_{growth} . (Fig. 3b,c). For J_{max} , however, there was no change in Ea_J , only a strong decline in
480 ΔS_J with increasing T_{growth} . (Fig. 3e, f).

481 We found no evidence to support adaptation of $Topt_V$, Ea_V and ΔS_V to climate of
482 origin as there were no significant trends observed with temperature at species' seed source
483 (i.e. T_{home}) in the common garden dataset (Fig. 4a, b, c). These observations were consistent
484 with the lack of significant trends for $Topt_A$ in the common garden dataset. However, $Topt_J$
485 and ΔS_J showed significant trends with T_{home} (Fig. 4d, e, f; Table 1), suggesting adaptation of
486 both parameters to climate of origin. The results were similar for the two alternative
487 definitions of the climate of origin (Table S2).

488

489 *The balance between J_{max} and V_{cmax}*

490 We found no detectable correlation between T_{growth} and the basal rate of V_{cmax} at a
491 standard temperature 25°C for mature plants in their natural habitats, but the basal rate of J_{max}
492 showed a strong decrease (Fig. 5a, b). The ratio of $J_{max}:V_{cmax}$ at 25°C (JV_r) showed a

493 significant decrease with increasing T_{growth} (Fig. 5c, Table 1). We excluded the Scots pine,
494 Finland dataset when fitting linear regression as the JV_r value significantly departed from the
495 general trend, and was therefore identified as an outlier (black circle in Fig. 5c).

496 Basal rates of V_{cmax} and J_{max} did not show significant trends with T_{growth} , but JV_r
497 responded negatively to T_{growth} in the seasonal dataset (Fig. 5d: f). We found no evidence to
498 support adaptation of basal rates of V_{cmax} and J_{max} to climate of origin; no parameters showed
499 any significant trend with T_{home} in the common garden dataset (Fig. 5g, h, Table 1). However,
500 there was evidence of adaptation of JV_r to climate of origin, as JV_r showed a significant
501 decrease with T_{home} in the common garden dataset (Fig. 5i, Table 1).

502

503 *Assessing the role of day respiration*

504 We found no detectable trends (Fig. S3, Table 1) for either R_{L25} or E_a of mature plants
505 in native environments. Similar results were found for common garden studies and no
506 seasonal trends were observed for either R_{L25} or E_a in the seasonal dataset. However, the data
507 showed a slight negative trend for $R_{L25}:V_{cmax25}$ ratio with increasing T_{growth} (of mature plants
508 in native environments) and T_{growth} (of seasonal datasets) (Fig. S4). Also we observed
509 negative E_a values in all three datasets (Fig. S4).

510

511 *Model to represent acclimation and adaptation in vegetation models*

512 Our results provide evidence that changes in the temperature response of
513 photosynthesis among datasets are principally driven by acclimation of photosynthetic
514 biochemistry to growth temperature. Both Ea_V and JV_r showed strong acclimation to growth
515 temperature with significant (albeit weak) acclimation of ΔS_V . We found little evidence to
516 support local adaptation of photosynthetic biochemistry to climate of origin. Only JV_r and
517 ΔS_J showed statistically significant, but weak signals of local adaptation. We further tested
518 whether variation in Ea_V and JV_r can explain the seasonal acclimation of temperature
519 optimum of photosynthesis observed in the seasonal dataset using linear regression analysis
520 (JV_r and Ea_V vs $Topt_{A275}$). We found a strong negative trend for the relationship between JV_r
521 and $Topt_{A275}$ (Fig. 6a). $Topt_{A275}$ increased by $\sim 6^\circ\text{C}$ for a unit decrease in JV_r . Also, we found
522 significant trend between Ea_V and $Topt_{A275}$; $Topt_{A275}$ increased by $\sim 0.2^\circ\text{C}$ for a unit increase
523 in Ea_V (Fig. 6b). Therefore, the observed trends in $Topt_A$ of mature plants in native habitats
524 (Fig. 1a) can be explained by the effect of growth temperature on Ea_V , ΔS_V , JV_r and the

525 effects of both growth temperature and climate of origin on ΔS_J and JV_r . Hence,
526 photosynthetic temperature acclimation and adaptation can be implemented in GVMs using
527 these parameters. Therefore, we modified the baseline peaked Arrhenius functions (Eqn 8) to
528 represent i) temporal variability of Ea_V and ΔS_V using Eqn 12, ii) geographical and temporal
529 variation of JV_r ratio at 25°C and ΔS_J using Eqn 13. The full final model is given in Table 2.

530 We found that the new temperature response functions were able to predict the
531 temperature optima of photosynthesis observed in field-grown mature plants with a high
532 degree of accuracy ($r^2=0.80$). The slope (1.09 ± 0.15) and intercept (-2.20 ± 4.10) of the linear
533 regression between the predicted and observed $Topt_A$ were not significantly different from
534 unity and zero respectively (Fig. 7a, Table S3). Our new model outperformed the Kattge &
535 Knorr (2007) algorithms, which tend to underpredict $Topt_A$ (Fig. 7b, Table S3). Further, the
536 use of PFT-specific values of V_{cmax} , together with a standard unacclimated photosynthetic
537 temperature responses (Leuning, 2002), was not able to predict the observed variability in
538 $Topt_A$ as it predicts a $Topt_A \approx 25^\circ\text{C}$ for all datasets (Fig 7a). Note that the mature plant dataset
539 was not included in fitting Eqn 11-13, so that the predicted $Topt_{A275}$ in Fig. 7a was
540 independent of the data used to derived the model parameters.

541

542 Discussion

543 We developed new mathematical functions to represent the photosynthetic temperature
544 response in vegetation models to account for both acclimation to growth temperature and
545 adaptation to climate of origin using a global database that contains more than 140 species.
546 We found acclimation to growth temperature to be the principal driver of the photosynthetic
547 temperature response, and observed only a few modest effects of adaptation to temperature at
548 the climate of origin. The observed variation of temperature optimum for leaf net
549 photosynthesis was primarily explained by the photosynthetic biochemical component
550 processes rather than stomatal or respiratory processes. The new temperature response
551 functions presented here capture the observed T_{opt_A} across biomes with higher degree of
552 accuracy than previously proposed algorithms.

553

554 *Adaptation of T_{opt_A} to climate of origin*

555 Despite a significant range in long term mean temperature at species' seed sources, we
556 found no predictable relationship for T_{opt_A} with climate of origin when species were grown
557 in common gardens. Therefore, our results do not support the hypothesis T_{opt_A} is adapted to
558 species' climate of origin (hypothesis 1). Our results contrast with previous studies which
559 found that T_{opt_A} is related to species climate of origin (Fryer & Ledig, 1972; Slatyer, 1977;
560 Slatyer, 1978; Robakowski *et al.*, 2012), but there are a number of studies which compare the
561 temperature response of photosynthesis and report a lack of local adaptation of T_{opt_A} (Ledig
562 & Korbobo, 1983; Gunderson *et al.*, 2000). We propose two hypotheses to explain the lack of
563 local adaptation of T_{opt_A} ; i) there is a lack of specialization in photosynthetic biochemistry in
564 relation to climate of origin and ii) the capacity of species to adjust their T_{opt_A} to temporal
565 variations in local thermal environment could mask ecotypic thermal adaptation of T_{opt_A}
566 (Robakowski *et al.*, 2012).

567 With respect to hypothesis (i), Rubisco activity is one of the key photosynthetic
568 biochemical determinants and one of the most temperature responsive physiological process
569 (Galmés *et al.*, 2015). Several lines of evidence suggest that Rubisco catalytic properties,
570 including the relative specificity for CO_2/O_2 ($S_{c/o}$), the Michaelis–Menten constants for CO_2
571 (K_c) and O_2 (K_o), and the maximum turnover of carboxylation (k_c), differ among species that
572 have evolved under different thermal environments (Andersson & Backlund, 2008; Galmes *et*
573 *al.*, 2014). However, it is not clear whether these differential responses are due to genetic

574 adaptation of Rubisco kinetics to climate of origin or to the temporal effects of growth
575 temperature. Galmés *et al.* (2015) argued that closely related species could be less adapted to
576 their current thermal environment due to past strategies that limit adaptation of Rubisco to
577 new thermal regimes (Lambers *et al.*, 2008). This hypothesis was further supported by Savir
578 *et al.* (2010) who suggested point mutations may not cause a significant improvement in
579 Rubisco activity due to its close optimality in the net photosynthetic rate (Tcherkez *et al.*,
580 2006). As a result, the adaptive evolution of Rubisco to novel thermal environments may be
581 rare, as adaptation to a local environment will be working against the selective pressure to
582 cope with seasonal and annual temperature variations and would reduce species fitness, and
583 expansion into new niches with different thermal environments. Other than the parameters
584 ΔS_J and JV_r , our results do not show evidence for thermal adaptation of photosynthetic
585 biochemical parameters. Thus we suggest that the lack of local adaptation of $Topt_A$ may be
586 partially explained by the lack of specialization in photosynthetic biochemistry, particularly
587 Rubisco kinetic properties to species climate of origin.

588 Regarding ii), we suggest that the capacity of Rubisco kinetic properties to adjust to
589 temporal variations in growth temperature could potentially mask the species' pre-adaptive
590 responses to their original thermal environments. Here, we show strong evidence for the
591 acclimation of $Topt_A$ to species T_{growth} which is primarily due to the variations in
592 photosynthetic biochemical component processes JV_r , Ea_V , ΔS_V and ΔS_J in relation to the
593 seasonal temperature dynamics. Potential mechanisms by which the kinetic properties of
594 Rubisco could be altered in response to changes in temperature include structural changes in
595 the Rubisco enzyme itself (Huner & Macdowall, 1979; Huner, 1985; Yamori *et al.*, 2006);
596 changes in the concentration of other photosynthetic enzymes such as Rubisco activase
597 (Yamori *et al.*, 2005, Yamori *et al.*, 2011); expression of cold/heat stable isozymes (Yamori *et al.*
598 *et al.*, 2006); and by alterations in membrane fluidity (Falcone *et al.*, 2004). A number of
599 previous studies have demonstrated short-term acclimation of Rubisco kinetics to growth
600 temperature (Medlyn *et al.*, 2002b; Yamori *et al.*, 2006; Kattge & Knorr, 2007; Lin *et al.*,
601 2013; Yamaguchi *et al.*, 2016; Smith & Dukes, 2017; Crous *et al.*, 2018) although the
602 sensitivities of the responses varied. In addition, studies that have compared the acclimation
603 capacity of multiple species in common growth temperatures have shown similar direction
604 and magnitude of short-term temperature acclimation of $Topt_A$ (Berry & Björkman, 1980;
605 Sendall *et al.*, 2015) and Rubisco kinetics (Lin *et al.*, 2013; Smith & Dukes, 2017) across
606 species irrespective of their climate of origin. Therefore, we argue that the capacity of
607 species to adjust their photosynthetic biochemistry to temporal variations in growth

608 temperature provides a fitness advantage over that of local climatic adaptation of T_{opt_A} and
609 its related mechanisms, by enabling species to optimize carbon balance in their current
610 habitat (Hikosaka *et al.*, 2006).

611 The lack of a temperature adaptation response in this study contrasts with the results of
612 a previous meta-analysis which found both evolutionary changes and an acclimation effect on
613 T_{opt_A} (Yamori *et al.*, 2014). Our common garden studies compared closely related species (or
614 provenances of the same species) in most cases. The most climatically divergent sets of
615 species included in this study were those of Vårhammar *et al.* (2015) (lowland and montane
616 tropical species) and Dillaway and Kruger (2010) (North American boreal and temperate
617 deciduous species; see Table S1). In contrast, Yamori *et al.* (2014) compared temperature
618 responses of C_3 , C_4 and CAM plants and found evidence of evolutionary shifts among these
619 functional groups. Other common garden studies with taxonomically diverse species have
620 also provided evidence for evolutionary changes in T_{opt_A} in relation to climate of origin
621 (Cunningham & Read, 2002; Reich *et al.*, 2015).

622

623 *Acclimation of T_{opt_A} to growth temperature*

624 Our observations of seasonal photosynthetic temperature response datasets suggest that
625 the seasonal plasticity in T_{opt_A} is principally driven by (i) the adjustment of the temperature
626 response of the Rubisco limited photosynthetic rate and (ii) the balance between Rubisco
627 limited and electron transport limited photosynthetic rates. These two mechanisms control the
628 seasonal shifts in T_{opt_A} as follows. First, at biologically relevant leaf temperatures, the light
629 saturated net photosynthetic rate is mostly limited by Rubisco activity (Rogers & Humphries,
630 2000; De Kauwe *et al.*, 2016; Yamaguchi *et al.*, 2016). An increase in E_{aV} along with a
631 decrease in ΔS_V increases the Rubisco-limited photosynthetic rate with temperature, and thus
632 affects the shape of the photosynthetic temperature response. The rate of increase in E_{aV} with
633 T_{growth} in this study ($1.14 \text{ kJ mol}^{-1} \text{ }^\circ\text{C}^{-1}$) aligns closely with previous reports (Hikosaka *et al.*,
634 2006: $1.01 \text{ kJ mol}^{-1} \text{ }^\circ\text{C}^{-1}$). A number of potential causes have been suggested for variations in
635 E_{aV} across species, including mesophyll conductance to CO_2 diffusion (Bernacchi *et al.*,
636 2002; Warren *et al.*, 2007; Walker *et al.*, 2013; von Caemmerer & Evans, 2015), kinetic
637 properties of Rubisco (Yamori *et al.*, 2006), distribution of leaf nitrogen among
638 photosynthetic proteins (Yin *et al.*, 2018) and the influence of other enzymes that affect the *in*
639 *vivo* activity of Rubisco (Onoda *et al.*, 2005). Further, the Rubisco activation status could also

640 be a significant factor contributing to the observed trends in Ea_V with T_{growth} as evidence
641 suggested that, plants have the capacity to maintain high Rubisco activation status through an
642 increase in Rubisco activase concentration and expression of heat stable Rubisco activase
643 isoforms (Crafts-Brandner & Salvucci, 2000; Sage *et al.*, 2008; Yamori *et al.*, 2014).
644 However, not all authors find a change in Ea_V with growth temperature. Kattge and Knorr
645 (2007) did not find any temperature acclimation in Ea_V . They argued that the choice of a
646 standard, rather than peaked, Arrhenius model to fit the temperature response for V_{cmax}
647 without considering the deactivation energy would be a possible reason for the observed
648 acclimation responses of Ea_V in previous studies (e.g. Hikosaka *et al.* 2006). However, here
649 we used the peaked Arrhenius model, and thus the acclimation of Ea_V that we observed is not
650 an artifact of model choice.

651 The second important mechanism for acclimation was a change in the magnitude of
652 JV_r , as has also been observed by (Kattge & Knorr, 2007; Crous *et al.*, 2013; Lin *et al.*, 2013;
653 Crous *et al.*, 2018). The ratio determines the transition between the two limiting steps, W_c and
654 W_j . As the temperature responses of W_c and W_j are different from each other with different
655 optimum temperatures ($Topt$ of $W_c < Topt$ of W_j), $Topt_A$ is potentially determined by the
656 limiting step (von Caemmerer & Farquhar, 1981; Hikosaka, 1997). At higher JV_r , the
657 photosynthetic rate is mostly limited by RuBP carboxylation, therefore, $Topt_A$ tends to be a
658 lower value and vice versa.

659 The acclimation capacity of ΔS_V observed in this study ($-0.38 \text{ J mol}^{-1} \text{ K}^{-1}$) was lower
660 compared to the $-1.07 \text{ J mol}^{-1} \text{ K}^{-1} \text{ }^\circ\text{C}^{-1}$ reported in (Kattge & Knorr, 2007). The higher
661 sensitivity observed in Kattge and Knorr (2007) would potentially be explained by the lack of
662 variation in Ea_V . Both Ea_V and ΔS_V are correlated: a high sensitivity in Ea_V to T_{growth} would
663 potentially cause ΔS_V to be less sensitive and vice versa.

664 We observed changes in JV_r with temperature in all three datasets (Fig. 5), but only the
665 mature plant dataset showed a change in either of the two terms contributing to this ratio. In
666 this dataset, the reduction in JV_r is driven by a reduction in J_{max25} , whereas in the other two
667 datasets, there is no overall effect on either V_{cmax25} or J_{max25} . Some previous studies have
668 observed changes in V_{cmax25} with growth temperature in more limited datasets (Way & Oren,
669 2010; Lin *et al.*, 2013; Ali *et al.*, 2015; Scafaro *et al.*, 2017; Crous *et al.*, 2018; Smith &
670 Dukes, 2018), but here we did not find any consistent pattern in V_{cmax25} . It appears that JV_r
671 responded strongly and consistently to growth temperature, but whether this is achieved by
672 increasing V_{cmax} , decreasing J_{max} , or both, is highly variable. We speculate that the global
673 pattern in J_{max} observed in Figure 5b may be a response to increasing light availability in the

674 tropics, following the co-limitation hypothesis, as proposed by Dong *et al.* (2017), rather than
675 a response to growth temperature.

676

677 *Improved temperature response functions for photosynthetic capacity*

678 We demonstrate acclimation to growth temperature to be the principal driver, and only
679 a few modest effects of adaptation, in photosynthetic temperature responses at global scale.
680 Our results highlight the limitation of using a fixed set of parameters to determine T_{opt_A} , and
681 challenge the use of PFT-specific V_{cmax25} and J_{max25} with a fixed set of temperature response
682 parameters without accounting for temperature acclimation and adaptation (Leuning, 2002) in
683 global vegetation models (Harper *et al.*, 2016; Rogers *et al.*, 2017a). We also demonstrate
684 that the current representation of photosynthetic temperature acclimation (Kattge & Knorr,
685 2007) that has been implemented in some vegetation models (Smith & Dukes, 2013;
686 Lombardozzi *et al.*, 2015; Smith *et al.*, 2016), was not able to predict the observed patterns in
687 T_{opt_A} across biomes.

688 We proposed new algorithms for temperature response that are based on a broad range
689 of data, account for both geographical and temporal variability in photosynthetic biochemical
690 component processes, and are able to capture observed variation of T_{opt_A} across biomes with
691 a high degree of accuracy. The temperature response functions that we propose have a broad
692 temperature domain ($\sim 3 - 37$ °C) which should enable their use in GVMs without outer
693 domain uncertainties (Stinziano *et al.*, 2017)), a limitation of the algorithms proposed
694 previously (Katte & Knorr, 2007) that are widely implemented in GVMs (BETHY, CLM4.5,
695 Orchidee). Due to these advantages, our new photosynthetic temperature algorithms provide
696 an improved representation of geographical and temporal variability in T_{opt_A} and should
697 ultimately improve the accuracy of predicted future C cycle in GVMs.

698

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719 **Author contribution statement**

720 Project conceived by BEM. Analyses designed and carried out by DPK with guidance from
721 BEM, JED, MGT, and contributions from MGD. Manuscript writing led by DK, BEM and
722 JED. All co-authors contributed data, ideas, and edited the manuscript.

723

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965 **Supporting Information**

966 **Fig. S1** Distribution of the dataset used in this study

967 **Fig. S2** Relationship between apparent V_{cmax} and J_{max} values derived using two AC_i curve
968 fitting routines; with and without accounting for TPU limitation

969 **Fig. S3** Temperature response parameters of photosynthetic respiratory component
970 processes

971 **Fig. S4** $R_{L25}:V_{\text{cmax}25}$ ratio at a standard leaf temperature 25°C

972 **Table S1** List of data sources

973 **Table S2** Results of the linear mixed effect models fitted for common garden dataset to test
974 for adaptation of photosynthetic temperature response parameters to species' climate of
975 origin

976 **Table S3** Results of the linear regression analysis between observed and modelled
977 temperature optimum for photosynthesis at a fixed C_i of 275 $\mu\text{mol mol}^{-1}$ using model
978 parameterizations given in Table 2 in the main text and Kattge and Knorr (2007) algorithm.

979 **Figure Legends**

980 **Figure 1** Temperature optimum for (a, b, c) leaf net photosynthesis (T_{optA}) and (d, e, f) net
981 photosynthesis at an intercellular CO_2 concentration of $275 \mu\text{mol mol}^{-1}$ ($T_{optA275}$) of mature
982 plants growing in their native environments (a, d), species in field (grown at ambient growth
983 temperatures) measured at least in two or more seasons (b, e) and species or provenances
984 from contrasting climates of origin grown in common growth temperatures (common gardens
985 or controlled environments; c,f) . T_{growth} is the mean air temperature of preceding 30 days.
986 T_{home} is the long-term (1960-1990) mean maximum temperature of the warmest month at
987 species' seed origin. Different colours in panels (a,b) depict Plant Functional Types: orange,
988 Tropical evergreen angiosperms (EA-Tr); light blue, Arctic tundra; red, Temperate deciduous
989 angiosperms (DA-Te); blue, Temperate evergreen angiosperms (EA-Te); green, Boreal
990 evergreen gymnosperms (EG-Br); purple, Temperate evergreen gymnosperms (EG-Te); in
991 panels (c, d, e, f) different datasets. The thick black lines in each panel are (a, d) least-
992 squares linear regression fits; (b, c, e, f) linear mixed-effect model fits with random intercepts
993 for each dataset. The thin lines in respective colours are the fitted random intercept models
994 for individual datasets. Error bars represent $\pm 1\text{SE}$.

995 **Figure 2** Biochemical temperature response parameters for the Mature plants dataset in
996 relation to mean air temperature of preceding 30 days (T_{growth}). Different colours represent
997 Plant Functional Types as in Fig. 1(a, d). Solid and dotted lines in each panel are the least-
998 squares linear regression fits (this study; coefficients and r^2 values given in Table 1) and the
999 linear models proposed by Kattge and Knorr (2007) respectively. Error bars represent $\pm 1\text{SE}$.
1000 Legend follows Fig. 1(a, d).

1001 **Figure 3** Biochemical temperature response parameters for the Seasonal dataset in relation
1002 to mean air temperature of preceding 30 days (T_{growth}). Data were measured on field-grown
1003 plants (including whole-tree chamber experiments) in two or more seasons. Solid and dotted
1004 lines in each panel are the linear mixed-effect model fits (this study; coefficients and r^2
1005 values are given in Table 1) and the linear models proposed by Kattge and Knorr (2007)
1006 respectively. Error bars represent $\pm 1\text{SE}$. Legend follows Fig. 1(b, e).

1007 **Figure 4** Biochemical temperature response parameters for the Common garden dataset in
1008 relation to the long-term (1960-1990) mean maximum temperature of the warmest month at
1009 species' seed origin (T_{home}). Data were measured in species or provenances from contrasting
1010 climates of origin grown at common growth temperatures (common gardens and controlled

1011 environments). Solid lines in each panel are the linear mixed-effect model fits (this study;
1012 coefficients and r^2 values are given in Table 1). Error bars represent ± 1 SE. Legend follows
1013 Fig. 1(c, f).

1014 **Figure 5** V_{cmax} , J_{max} and $J_{max} \cdot V_{cmax}$ ratio (JV_r) at a standard leaf temperature (25 °C) of
1015 (a,b,c) mature plants growing in their native environments; (d,e,f) field-grown plants
1016 measured in two or more seasons; and (g,h,i) species or provenances from contrasting
1017 climates of origin grown in common growth temperatures (common gardens or controlled
1018 environments). T_{growth} is the mean air temperature of preceding 30 days. T_{home} is the long-
1019 term (1960-1990) mean maximum temperature of the warmest month at species' seed origin
1020 respectively. Solid lines in each panel are the least-squares linear regression fits (panels b and
1021 c), linear mixed-effect model fits with random intercepts for each dataset (panels f and i).
1022 One outlier is circled in (c) (see text). Error bars represent ± 1 SE. Legend follows Fig. 1.

1023 **Figure 6** Relationship between JV_r and temperature optimum for photosynthesis at a fixed
1024 intercellular CO₂ concentration of 275 $\mu\text{mol mol}^{-1}$ ($Topt_{A275}$) (a) and relationship between Ea_V
1025 and $Topt_{A275}$ (b). Data were measured on field-grown plants (including whole-tree chamber
1026 experiments) in two or more seasons. Lines in each panel are the linear mixed effect
1027 regression model fits (in panel a, $Topt_{A275} = 35.78 - 5.93 \times JV_r$; $R^2=0.36$, in panel b,
1028 $Topt_{A275} = 13.11 + 0.20 \times Ea_{Vcmax}$; $R^2=0.49$. Error bars represents ± 1 SE.

1029 **Figure 7** Observed and modelled temperature optimum for photosynthesis at a fixed C_i of
1030 275 $\mu\text{mol mol}^{-1}$ using model parameterizations given in Table 2. (a) With acclimation and
1031 adaptation functions developed in this study ($y = 1.09x - 2.20$, $r^2=0.80$), (b) Kattge and
1032 Knorr (2007) acclimation function ($y = 1.58x - 13.82$, $r^2=0.83$). The crossed circle in the x-
1033 axis of panel a depicts the predicted $Topt_{A275}$ with a fixed set of parameters without
1034 acclimation and adaptation (Leuning, 2002). Thin lines: 1:1 relationship; Thick lines: least-
1035 squares regression fit. In panel a, the intercepts and the slope of the linear regression were not
1036 significantly different from zero and unity respectively (Table S3). Error bars represent ± 1 SE.

1037 **Table 1.** Results of the linear regression analysis of the parameters of Eqn 1, 8 and 9. For common garden and seasonal datasets, linear mixed
1038 models were fit accounting for between datasets variations of a given parameter (see materials and methods for details). For mature plants in
1039 native environments, parameter values were derived by fitting simple linear regression models (Eqn 10). Values in parentheses are standard
1040 errors of estimates. Bold values are the significant parameters at $\alpha = 0.05$

1041

Parameter	Mature plants in native environment (Eqn 10)				Seasonal dataset (Eqn 11)					Common garden dataset (Eqn 12)				
	<i>a</i>	<i>b</i>	<i>r</i> ²	P-value	<i>A</i> _{ac}	α _{ac}	<i>r</i> ² (Marginal)	<i>r</i> ² (Conditional)	P-value	<i>A</i> _{ad}	α _{ad}	<i>r</i> ² (Marginal)	<i>r</i> ² (Conditional)	P-value
<i>Topt_A</i>	12.5 (1.4)	0.62 (0.1)	0.80	<0.001	18.2 (1.1)	0.34 (0.05)	0.27	0.87	<0.001	24.8 (2.1)	0.07 (0.1)	0.01	0.71	0.309
<i>Topt_{A275}</i>	14.9 (1.5)	0.63 (0.1)	0.84	<0.001	20.5 (1.2)	0.24 (0.05)	0.16	0.85	<0.001	26.8 (2.3)	0.07 (0.1)	0.03	0.30	0.400
<i>Biochemical parameters</i>														
<i>V_{cmax25}</i>	85.3 (16.7)	-1.84 (0.8)	0.19	0.404	58.2 (12.0)	0.50 (0.4)	0.01	0.94	0.252	33.4 (28.0)	1.62 (0.9)	0.07	0.91	0.096
<i>J_{max25}</i>	194.7 (24.1)	-5.13 (1.2)	0.53	<0.001	141.3(18.8)	-1.35 (0.7)	0.03	0.95	0.053	92.7 (47.2)	1.63 (1.6)	0.02	0.95	0.312
<i>Ea_V</i>	48.7 (7.8)	0.82 (0.4)	0.14	0.067	39.7 (6.2)	1.14 (0.3)	0.32	0.91	<0.001	79.4 (13.1)	-0.37 (0.5)	0.14	0.14	0.450
<i>Ea_J</i>	43.5 (9.8)	-0.19 (0.5)	0.05	0.7143	27.2 (5.0)	0.26 (0.3)	0.04	0.82	0.325	51.5 (8.7)	-0.38 (0.3)	0.20	0.20	0.247
ΔS_V	662.0 (8.7)	-1.31 (0.5)	0.30	0.011	645.1 (4.6)	-0.38 (0.2)	0.09	0.82	0.089	647.9 (9.5)	-0.36 (0.3)	0.08	0.66	0.302
ΔS_J	667.3 (7.8)	-1.34 (0.4)	0.36	0.005	653.9 (4.6)	-0.85 (0.2)	0.22	0.94	<0.001	662.3 (7.5)	-0.99 (0.3)	0.49	0.84	<0.001
<i>Topt_V</i>	24.3 (3.8)	0.71 (0.2)	0.40	0.002	30.3 (1.9)	0.36 (0.1)	0.23	0.77	<0.001	34.3 (3.3)	0.12 (0.1)	0.05	0.36	0.335
<i>Topt_J</i>	19.9 (2.9)	0.63 (0.2)	0.52	<0.001	27.6 (1.8)	0.31 (0.1)	0.13	0.91	<0.001	24.8 (3.4)	0.42 (0.1)	0.42	0.60	<0.001
<i>JV_r</i>	2.9 (0.2)	-0.06 (0.01)	0.66	<0.001	2.3 (0.2)	-0.03 (0.01)	0.07	0.17	<0.001	2.5 (0.3)	-0.03 (0.01)	0.13	0.64	0.005
<i>Respiratory parameters</i>														
<i>R_{L25}</i>	2.8 (0.5)	-0.09 (0.03)	0.38	0.0037	1.54 (0.42)	-0.01 (0.02)	0.01	0.25	0.502	1.16 (0.45)	0.01 (0.01)	0.01	0.61	0.583
<i>Ea</i>	-20.7 (14.3)	1.18 (0.78)	0.07	0.1508	-9.17 (11.49)	0.42 (0.61)	0.02	0.83	0.485	-4.25 (43.38)	0.12 (1.57)	0.01	0.93	0.937
<i>R_{L25}:V_{cmax25}</i>	0.036 (0.01)	-0.001 (0.0003)	0.22	0.033	0.03 (0.01)	(0.0003)	0.04	0.60	0.043	0.03 (0.01)	(0.0004)	0.06	0.53	0.149

1042 **Table 2.** Parameters of the temperature acclimation and adaptation functions developed in this study. T_{home} is the long-term (1960-1990) mean
 1043 maximum temperature of the warmest month, T_{growth} is the mean air temperature of preceding 30 days. Plant Functional Types, DA-Te:
 1044 deciduous angiosperms (temperate), EA-Te: evergreen angiosperms (temperate), EG-Te: evergreen gymnosperms (temperate), EG-Br: evergreen
 1045 gymnosperms (boreal), EA-Tr: evergreen angiosperms (tropical) and Arctic tundra: Arctic spp

Parameter	Model representation	Value	Units
V_{cmax25}	PFT specific	DA-Te	39.0
		EA-Te	82.9
		EG-Te	42.8
		EG-Br	80.4
		EA-Tr	39.4
		Arctic tundra	78.3
J_{max25}	Acclimation + Adaptation	$V_{cmax25} \times J_{V_r}$	$\mu\text{mol m}^{-2}\text{s}^{-1}$
J_{V_r}	Acclimation + Adaptation	$2.56 - 0.0375T_{home} - 0.0202(T_{growth} - T_{home})$	unitless
E_{aV}	Acclimation	$42.6 + 1.14T_{growth}$	kJ mol^{-1}
E_{aJ}	Global mean	40.71	kJ mol^{-1}
ΔS_v	Acclimation	$645.13 - 0.38T_{growth}$	$\text{J mol}^{-1} \text{K}^{-1}$
ΔS_J	Acclimation + Adaptation	$658.77 - 0.84T_{home} - 0.52(T_{growth} - T_{home})$	$\text{J mol}^{-1} \text{K}^{-1}$

1046