### 25 Abstract

Although plant photosynthetic capacity as determined by the maximum carboxylation 26 rate (i.e.,  $V_{c,max25}$ ) and the maximum electron transport rate (i.e.,  $J_{max25}$ ) at a reference temperature 27 (generally 25°C) is known to vary substantially in space and time in response to environmental 28 conditions, it is typically parameterized in Earth system models (ESMs) with tabulated values 29 associated to plant functional types. In this study, we developed a mechanistic model of leaf 30 utilization of nitrogen for assimilation (LUNA V1.0) to predict the photosynthetic capacity at the 31 global scale under different environmental conditions, based on the optimization of nitrogen 32 33 allocated among light capture, electron transport, carboxylation, and respiration. The LUNA model was able to reasonably capture the observed patterns of photosynthetic capacity as it 34 explained approximately 55% of the variation in observed  $V_{c,max25}$  and 65% of the variation in 35 observed  $J_{max25}$  across the globe. Our model simulations under current and future climate 36 conditions indicated that simulations of  $V_{c,max25}$  based on this new optimization strategy were 37 most affected in high-latitude regions under a warming climate and that ESMs using a fixed 38  $V_{c,max25}$  or  $J_{max25}$  by plant functional types were likely to substantially overestimate future global 39 photosynthesis. 40

41



44 1. Introduction

Photosynthesis is one of the major components of the ecosystem carbon cycle (Canadell 45 46 et al., 2007; Sellers et al., 1997) and is thus central to Earth system models (ESMs) (Block and Mauritsen, 2013; Hurrell et al., 2013). Most of the ESMs are based on photosynthesis models 47 developed by Farquhar et al. (1980), which are particularly sensitive to photosynthetic capacity. 48 The maximum carboxylation rate scaled to 25°C [i.e.,  $V_{c,max25}$  (µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>)] and the 49 maximum electron transport rate scaled to  $25^{\circ}$ C [i.e.,  $J_{max25}$  (µmol electron m<sup>-2</sup> s<sup>-1</sup>)] have been 50 generally accepted as the measure of photosynthetic capacity.  $V_{c,max25}$  and  $J_{max25}$  are the key 51 biochemical parameters in the photosynthesis models as they control the carbon fixation process 52 (Farquhar et al., 1980). There exist large variations in estimates of gross primary productivity in 53 space and time across ESMs (Schaefer et al., 2012), which have been partly attributed to 54 uncertainties in  $V_{c,max25}$  (Bonan et al., 2011). Accurate estimations of  $V_{c,max25}$  and  $J_{max25}$  are 55 needed to simulate gross primary productivity because errors of  $V_{c,max25}$  and  $J_{max25}$  may be 56 exacerbated when upscaling from leaf to ecosystem level (Hanson et al., 2004). 57

Our ability to make reliable predictions of  $V_{c,max25}$  and  $J_{max25}$  at a global scale is limited. 58 One of the reasons is that we do not have a complete understanding of the processes influencing 59  $V_{c,max25}$  and  $J_{max25}$  (Maire et al., 2012; Xu et al., 2012) despite the fact that  $V_{c,max25}$  has been 60 measured and studied more extensively than many other photosynthetic parameters (Kattge and 61 62 Knorr, 2007; Leuning, 1997; Wullschleger, 1993). Many empirical studies have shown that  $V_{c,max25}$  and  $J_{max25}$  (or field-based surrogates) correlate with leaf nitrogen content (Medlyn et al., 63 1999; Prentice et al., 2014; Reich et al., 1998; Ryan, 1995; Walker et al., 2014). Therefore, a 64 constant relationship between the leaf nitrogen content and  $V_{c,max25}$  or  $J_{max25}$  is commonly utilized 65 66 by many ecosystem models (Bonan et al., 2003; Haxeltine and Prentice, 1996; Kattge et al.,

2009). The relationship between leaf nitrogen content,  $V_{c,max25}$  and  $J_{max25}$  varies with different light, temperature, nitrogen availability and CO<sub>2</sub> conditions (Friend, 1991; Reich et al., 1995; Ripullone et al., 2003), and therefore, the prescribed relationship of  $V_{c,max25}$ ,  $J_{max25}$  and leaf nitrogen content might introduce significant biases into predictions of future photosynthetic rates, and also the downstream carbon cycle and climate processes that are dependent on these predictions (Bonan et al., 2011; Knorr and Kattge, 2005; Rogers, 2014).

To better account for the relationships between photosynthetic capacities and their 73 environmental determinants, we developed a mechanistic model of leaf utilization of nitrogen for 74 75 assimilation (LUNA V1.0) at the global scale that accounts for the key drivers (temperature, radiation, humidity, CO<sub>2</sub> and day length) contributing to the variability in the relationship 76 77 between leaf nitrogen,  $V_{c,max25}$  and  $J_{max25}$ . Based on the theoretically optimal amount of leaf nitrogen allocated to different processes, the LUNA model predicts  $V_{c,max25}$  and  $J_{max25}$  under 78 different environmental conditions. We estimate the LUNA model parameters by fitting the 79 model predictions to observations of  $V_{c,max25}$  and  $J_{max25}$ . In order to assess the impacts of future 80 climate change on photosynthesis, we used the calibrated LUNA model to estimate the summer 81 season net photosynthetic rate using predicted  $V_{cmax25}$  and  $J_{max25}$  under historical and future 82 83 climate conditions. We conclude that ESMs using a fixed  $V_{c,max25}$  or  $J_{max25}$  by plant functional types (PFTs) are likely to substantially overestimate future global photosynthesis. 84

85

### 86 2. Methodology

87 *2.1. Overview* 

Our *LUNA* model (version 1.0) is based on the nitrogen allocation model developed by Xu et al.
(2012), which optimizes nitrogen allocated to light capture, electron transport, carboxylation, and

90 respiration. Xu et al. (2012) considered a series of assumptions on the model to generate optimized nitrogen distributions, these were (i) that storage nitrogen is allocated to meet 91 requirements to support new tissue production; (ii) respiratory nitrogen is equal to the demand 92 implied by the sum of maintenance respiration and growth respiration; (*iii*) light capture, electron 93 transport and carboxylation are co-limiting to maximize photosynthesis. Xu et al.'s model needs 94 to be calibrated, and has thus far been tested for three sites. Here, we expand on the work of Xu 95 et al. (2012) to allow global predictions of nitrogen allocation, by fitting the model parameters to 96 an expanded photosynthetic capacity data set. To make global predictions feasible, we also made 97 98 important refinements to the model by considering the impacts of both day length and humidity, and the variations in the balance between light-limited electron transport rate and the Rubisco-99 limited carboxylation rate in accordance with recent theory. We used an efficient Markov Chain 100 101 Monte Carlo simulation approach, the Differential Evolution Adaptive Metropolis Snooker Updater (DREAM-ZS) algorithm (Laloy and Vrugt, 2012), to fit the nitrogen allocation model to 102 a large dataset of observed  $V_{c,max}$  and  $J_{max}$  collected across a wide range of environmental 103 gradients (Ali et al., 2015). After model fitting, a sensitivity analysis was performed to gauge the 104 response of the model to parametric variation and to environmental drivers (temperature, 105 photosynthetic active radiation, day length, relative humidity and atmospheric CO<sub>2</sub> 106 concentration). Finally, using climate projections from the Community Climate System Model 107 (CCSM), mean summer-season  $V_{cmax25}$  and  $J_{max25}$  and their impacts on net photosynthesis were 108 109 estimated for the globe.

110 *2.2. Model description* 

111 The structure of *LUNA* model is based on Xu et al. (2012), where plant leaf nitrogen is divided 112 into four pools: structural nitrogen, photosynthetic nitrogen, storage nitrogen and respiratory

nitrogen. We assume that plants optimize their nitrogen allocation to maximize the net 113 photosynthetic carbon gain, defined as the gross photosynthesis (A) minus the maintenance 114 respiration for photosynthetic enzymes  $(R_{psn})$ , under specific environmental conditions and given 115 the leaf nitrogen use strategy determined by four parameters in the LUNA model. These four 116 parameters in the model include 1)  $J_{maxb0}$  (unitless) specifies baseline proportion of nitrogen 117 allocated for electron transport rate; 2)  $J_{maxb1}$  (unitless) determines electron transport rate 118 response to light; 3)  $t_{c,i0}$  (unitless) specifies the baseline ratio of Rubisco-limited rate to light-119 limited rate; and 4) H (unitless) determines electron transport rate response to relative humidity. 120 121 The model uses area-based leaf nitrogen content and different environmental conditions (temperature, CO<sub>2</sub>, radiation, relative humidity and day length) as model inputs and predicts 122  $V_{c,max\,25}$  and  $J_{max25}$  based on the optimal amount of nitrogen allocated to different processes. 123

It is important to point out that the optimization in LUNA model is a conditional optimization 124 given the plant's nitrogen use strategies built into the model. Thus, it is possible that "optimal" 125 values of  $V_{c,max 25}$  and  $J_{max25}$  predicted by the LUNA model for future climate conditions could 126 have a lower net photosynthetic gain compared to fixed values of  $V_{c,max 25}$  and  $J_{max25}$ , where the 127 plant does not follow the nitrogen use strategies built into the LUNA model. An example is 128 shown in Fig. S1 where the "optimal" net photosynthetic carbon gain using the nitrogen 129 allocation predicted by LUNA model for the elevated temperature is lower than that using fixed 130 nitrogen allocation predicted for the ambient temperature. A complete description of the LUNA 131 132 model and the detailed associated optimization algorithms are provided in Appendix A. This optimality approach was introduced and tested by Xu et al. (2012) for only three test cases, and 133 here we assess its fidelity at large spatial scale with improvement to account for large scale 134 135 variability. Optimality approaches are important tools for land surface models, in that they

provide a specific testable hypothesis for plant function (Dewar, 2010; Franklin et al., 2012;
Schymanski et al., 2009; Thomas and Williams, 2014).

138

### 139 *2.3. Data and temperature* response *functions*

Details of data collection are stated in Ali et al. (2015). Specifically, we conducted a literature 140 search on Google Scholar to locate publications that included words " $V_{c,max}$ " or " $J_{max}$ " and also 141 contained "leaf nitrogen content", "maximum carboxylation rate", "maximum electron 142 transport rate", "leaf mass per area", or "specific leaf area". Individual values of  $V_{c,max}$ ,  $J_{max}$ , 143 area-based leaf nitrogen content (LNC<sub>a</sub>, g N/m<sup>2</sup> leaf) and leaf mass per unit leaf area (LMA, g 144 dry mass/ $m^2$  leaf) were then obtained by digitizing data from the literature. We used all of the 145 data from Ali *et al.* (2015) with the exception of one study that collected seasonal data on  $V_{c,max}$ 146 and  $J_{max}$  during prolonged drought (Xu and Baldocchi, 2003), in view that our model only 147 consider the optimal nitrogen allocation based on the monthly climate conditions but did not 148 consider the potential enzyme deterioration due to long-term droughts. In summary, we used 149 766 data points for  $V_{c,max}$  and 643 data points for  $J_{max}$  ranging from tropics to the arctic with a 150 total of 125 species. The data include evergreen and deciduous species from arctic, boreal, 151 temperate and tropical areas from different times of the season and different canopy locations 152 (Fig. S2). 153

To allow comparisons of  $V_{c,max}$  and  $J_{max}$  data collected at different temperatures, we first standardized data to a common reference temperature (25°C). To do this, we employed temperature response functions (TRFs). Because of issues related to the possibility of acclimation to temperature, the appropriate TRF to use is not yet a matter of scientific agreement (Yamori et al., 2006). To test the potential impact of our decision on the outcome of the study,

159 we used two alternative temperature response functions in this study. The first temperature response function (TRF1) used Kattge & Knorr's (2007)'s algorithm, which empirically accounts 160 for the potential for acclimation to growth temperature. Following the Community Land Model 161 version 4.5, the growth temperature is constrained between 11°C and 35°C (Oleson et al., 2013) 162 to limit the extent of acclimation to growth temperatures found in the calibration data set. The 163 second temperature response function (TRF2) did not consider change in temperature response 164 coefficients to growth temperature (Kattge and Knorr, 2007). See Appendix B for details of 165 166 TRF1 and TRF2.

Because the LUNA model is based on the  $C_3$  photosynthetic pathway, in this study, we only consider  $C_3$  species. Typically, plant species are grouped into several simple PFTs in ESMs because of computational limitations and gaps in the ecological knowledge. In view that the processes considered in *LUNA* model are universal across all  $C_3$  species and limited coverage of environmental conditions for individual plant functional types, our *LUNA* model does not differentiate among PFTs for  $C_3$  species. Namely, we have a single model for all  $C_3$  PFTs.

173 *2.4. Parameter estimation* 

The four parameters in the LUNA model are difficult to measure in the field. In this study, we 174 estimate these parameters by fitting out model against observations of  $V_{c,max25}$  and  $J_{max25}$  data 175 using the Differential Evolution Adaptive Metropolis (DREAM<sub>(ZS)</sub>) method (Vrugt et al., 2008, 176 2009; Laloy and Vrugt, 2012). We used the DREAM<sub>(ZS)</sub> algorithm (Vrugt et al., 2008, 2009; 177 178 Laloy and Vrugt, 2012) to calibrate our model because this method uses differential evolution as genetic algorithm for population evolution with a Metropolis selection rule to decide whether 179 candidate points should replace their parents or not. This simple Markov Chain Monte Carlo 180 181 (MCMC) method exhibits excellent sampling efficiencies on a wide range of model calibration problems, including multimodal and high-dimensional search problems. A detailed description of DREAM<sub>(ZS)</sub> appears in Vrugt et al., (2008, 2009) and Laloy and Vrugt (2012) and interested readers are referred to these publications. A simple Gaussian likelihood function (No.4 in DREAM<sub>(ZS)</sub>) was used to compare our model simulations of  $V_{c,max25}$  and  $J_{max25}$  with their observed counterparts. Examples of convergence of the parameters are presented in Fig. S3 and S4.

#### 188 *2.5. Model evaluations*

In this study, we considered two statistical metrics to analyze the performance of the LUNA model against the  $V_{c,max}$  and  $J_{max}$  data. They are the coefficient of determination  $(r^2)$  (Whitley et al., 2011) and the model efficiency (ME) (Whitley et al., 2011). The  $r^2$  is estimated using the linear regression model for observed values versus the predicted values. It measures the proportion of variance in  $V_{c,max}$  or  $J_{max}$  data explained by the model. The model efficiency is given as

ME = 
$$1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2}$$
,

where  $y_i$  are the observations,  $\hat{y}_i$  are the model estimates and  $\bar{y}$  is the mean of observations. It measures the proportion of variance in the  $V_{c,max}$  or  $J_{max}$  data explained by the 1:1 line between model predictions and observations (Mayer and Butler, 1993; Medlyn et al., 2005). The ME can range between 0 and 1, where a ME=1 corresponds to a 'perfect' match between modelled and measured data and a ME=0 indicates that the model predictions are only as accurate as the mean of the measured data.

# 201 *2.6. Model sensitivity analysis*

We conducted two sensitivity analyses of our model to identify the importance of the model parameters and the environmental variables. In the first sensitivity analysis, each value of the model parameter ( $J_{maxb0}$ ,  $J_{maxb1}$ ,  $t_{c,j0}$ , and H) was perturbed, one at a time, by +/-15% of their fitted values, to measure the importance of model parameters to modeled  $V_{c,max25}$  and  $J_{max25}$ . In the second sensitivity analysis, the environmental variables (day length (hours), daytime radiation (W m<sup>-2</sup>), temperature (°C), relative humidity (unitless), and carbon dioxide (ppm)) were perturbed, one at a time, by +/-15% of their mean values to identify which environmental variable was most likely to drive modeled  $V_{c,max25}$  and  $J_{max25}$ .

210

# 211 2.7. Changes in $V_{c,max25}$ and $J_{max25}$ under future climate projections

212 Global surface temperature by year 2100 (relative to present day) could increases by 3.9°C (Friedlingstein et al., 2014), with large variations across different regions of the globe (Raddatz 213 et al., 2007). Given the dependence of photosynthesis on temperature, it is critical to examine 214 how much future photosynthesis is likely to change in different regions. In this study, we aim to 215 investigate the importance of changes in  $V_{c,max25}$  and  $J_{max25}$  as predicted by the LUNA model to 216 the net photosynthesis rate  $(A_{net})$  estimation in future. The importance is measured by the 217 percentage difference in the estimation of future mean  $A_{net}$  for the top canopy leaf layer during 218 the summer season by using  $V_{c,max25}$  and  $J_{max25}$  estimated for historical climate conditions or the 219  $V_{c,max25}$  and  $J_{max25}$  estimated for future climate conditions (See Appendix C for details of  $A_{net}$ 220 221 calculation).

We used Coupled Climate Carbon Cycle Model Intercomparison Project Phase 5 (CMIP5) (Meehl et al., 2000) model outputs to obtain projections of the future climate. Climate modelers have developed four representative concentration pathways (RCPs) for the 21<sup>st</sup> century that correspond to different amounts of greenhouse gas emissions (Taylor et al., 2013). In this study, we used the historical and future climate conditions simulated by the CCSM 4.0 model 227 under the emission scenario of RCP8.5, which considers the largest greenhouse gas emissions. We did not consider other models and emission scenarios because our main purpose is to 228 estimate the potential impact of our nitrogen allocation model on photosynthesis estimation but 229 not to do a complete analysis under all CMIP5 output. Specifically, we used ten-year climate 230 conditions between 1995 and 2004 for historical and the ten-year climate conditions between 231 2090 and 2099 for future. We present optimal  $V_{c,max25}$  and  $J_{max25}$  predictions for the peak growing 232 season months. Data from the NOAA Earth System Research Laboratory over the years 1950 to 233 2010 (Riebeek, 2011) showed that the maximum amount of carbon dioxide drawn out of the 234 235 atmosphere occurs in August and February by the large land masses of Northern and Southern hemisphere, respectively. As a result, June, July and August months were used in this study as 236 the summer season for Northern hemisphere and December, January and February months were 237 considered as the summer season for the Southern Hemisphere.  $V_{cmax25}$  and  $J_{max25}$  were predicted 238 using the average values of the climate variables for June, July, August and November, 239 December, January for Northern, Southern hemispheres, respectively. 240

In order to identify the importance of changes in different climate variables (temperature, 241  $CO_2$ , radiation and relative humidity) to modeled changes in  $V_{c,max25}$  and  $J_{max25}$  in the future, we 242 243 conducted a third sensitivity analysis to investigate the impact of changes in climate variables on model results. In contrast to the previous two sensitivity analyses that focus on the mean current 244 climate conditions, the purpose of the third sensitivity analysis was to explore the global pattern 245 246 in sensitivity of  $V_{c,max25}$  and  $J_{max25}$  to changes in climate variables across different biomes of the globe in the future. Specifically, we measured the importance of changes in a specific climate 247 248 variable by the difference in  $V_{c,max25}$  and  $J_{max25}$  predicted by the LUNA model driven by historical

values or future values of the specific climate variable of interest with all other climate variablesset as their historical values.

251

### 252 **3. Results**

# 253 3.1. Model-data comparison of $V_{c,max25}$ and $J_{max25}$

The DREAM inversion approach allowed us to estimate the four parameters in our LUNA model 254 (Table 1). Using the fitted model parameters, the LUNA model explained 54% of the variance 255 of observed  $V_{c,max25}$  across all of the species (Fig. 1a) and 65% of the variance in observed  $J_{max25}$ 256 257 (Fig. 1b) using temperature response function TRF1 ( a temperature response function that considered the potential of acclimation to growth temperature). When temperature response 258 function TRF2 (a temperature response function that did not consider change in temperature 259 response coefficients to growth temperature) was used, the LUNA model explained 57% of 260 variance in observed  $V_{c,max25}$  (Fig. 1c) and 66% of the variance in observed  $J_{max25}$  (Fig. 1d) across 261 all of the species. By comparing the model predictions with only the studies that reported 262 seasonal cycles of  $V_{c,max25}$  and  $J_{max25}$ , we found the model explained 67 and 53% of the variance 263 in observed  $V_{c,max25}$  and  $J_{max25}$ , respectively, when TRF1 was used (see Fig. S5 a, b in the 264 supplementary file). The model explained 67 and 54% of the variance in observed  $V_{c,max25}$  and 265  $J_{max25}$ , respectively, when TRF2 was used (Fig. S5 c, d). 266

Our model also performed well for different PFTs. When using TRF1, for herbaceous plants, the LUNA model explained about 57% of the variance in observed  $V_{c,max25}$  (Fig. S6a). The model explained about 58 and 47% of the variance in observed  $V_{c,max25}$  for shrubs (Fig. S6b) and for trees (Fig. S6c), respectively. For the electron transport, the LUNA model explained about 49, 85 and 46% of the variances in observed J<sub>max25</sub> for herbaceous plants (Fig. S6d), shrubs (Fig.
S6e) and trees (Fig. S6f), respectively.

When we used a fixed temperature response curve under different growth temperatures (TRF2), for shrubs, the LUNA model has a slightly higher predictive power. It explained about 63% of the variances in observed  $V_{c,max25}$  (Fig. S7 b). Across TRF1 and TRF2, the LUNA model explained similar amount of variance in observed  $V_{c,max25}$  for herbaceous and trees (Fig. S7 a, c). For  $J_{max25}$ , the LUNA model explained a similar amount of variability for herbaceous, shrubs and trees for TRF1 (Fig. S6 d-f) and TRF2 (Fig. S7 d-f).

279

# 280 *3.2. Model sensitivity analysis*

Sensitivity analysis of the four model parameters (Table 1) showed that all the four parameters 281 had positive effects on  $V_{c,max25}$  (Fig. 2 a, c) and  $J_{max25}$  (Fig. 2 b, d) regardless of the temperature 282 response function used.  $t_{c,j_0}$  had the strongest effect on  $V_{c,max25}$  (Fig. 2 a, c) while  $J_{maxb0}$  had the 283 strongest effect on  $J_{max25}$  (Fig. 2 b, d). H had little impact on either  $V_{c,max25}$  and  $J_{max25}$  (Fig. 2 a-d). 284 Sensitivity analysis of the climate variables showed that, under both temperature response 285 286 functions (TRF1 and TRF2), the key drivers of change in  $V_{c,max25}$  were radiation, day length, temperature, CO<sub>2</sub> and relative humidity in order of decreasing importance (Fig. 3 a, c). For 287  $J_{max25}$ , the main drivers of change in  $J_{max25}$  were day length, temperature, radiation, relative 288

humidity and  $CO_2$  in order of decreasing importance (Fig. 3 b, d), irrespective of which temperature response functions were used.

291

# 292 3.3. Impacts of climate change on $V_{c,max25}$ and $J_{max25}$

Across the globe, the gradient of  $V_{c,max25}$  and  $J_{max25}$  is similar irrespective of whether TRF1 or 293 TRF2 was used (Fig. 4 and Fig. S8). Under historical conditions, regions from higher latitudes 294 are predicted to have relatively high  $V_{c,max25}$  and  $J_{max25}$  while lower latitudes are predicted to have 295 relatively low V<sub>c,max25</sub> and J<sub>max25</sub> (Fig. 4a,c for TRF1; Fig. S8a, c for TRF2). Future climatic 296 conditions are likely to decrease  $V_{c,max25}$  in many continents mainly due to the predicted increase 297 298 in temperature and CO<sub>2</sub> concentration (Fig. 4b for TRF1; Fig. S8b for TRF2).  $J_{max25}$  is predicted to decrease at higher latitudes but slightly increasing at lower latitudes (Fig. 4d for TRF1and Fig. 299 S8b for TRF2). 300

Our results showed that  $V_{c,max25}$  was most sensitive to CO<sub>2</sub>, temperature, radiation and relative humidity in order of decreasing importance (Fig. 5 a-d for TRF1 and Fig. S9a-d for TRF2).  $J_{max25}$  was most sensitive to temperature, radiation, relative humidity and CO<sub>2</sub> in order of decreasing importance (Fig. 6 a-d for TRF1 and Fig. S10a-d for TRF2). Across the globe, temperature had negative impacts on  $V_{c,max25}$  when using TRF1 (Fig. 5a); however,  $V_{c,max25}$  was found to be increasing at the lower latitudes when using TFR2 (Fig. S9a).

Our model showed that the future summer-season mean photosynthetic rate at the top leaf layer could be substantially overestimated if we does not consider the acclimation of  $V_{c,max25}$  and  $J_{max25}$  for the future (i.e., using the  $V_{c,max25}$  and  $J_{max25}$  estimated for historical climate conditions) (Fig. 7a, b), especially for regions with high temperatures (Fig. S11). Compared to the model using TRF1, the overestimation of future summer-season mean photosynthesis rates is much higher than the model using TRF2 (Fig. 7b). The overestimation of total global net photosynthetic rate is 10.1 and ~16.3% for TRF1 and TRF2, respectively.

314

#### 315 4. Discussion

The assumption that nitrogen is allocated according to optimality principles explained a large 317 part of variability in  $V_{c,max25}$  (~55%) and in  $J_{max25}$  (~65%) at the global scale, regardless of the 318 temperature response functions used. It also captured well the seasonal cycles and the PFT-319 specific values of  $V_{c,max25}$  and  $J_{max25}$  (Fig. S5-7). It has a much improved fitting to the data 320 321 compared to a multi-linear regression model using  $LNC_a$  and LMA as predictors, which only explained ~22% of the variance in observed  $V_{c,max25}$  (Fig. S12 a, d) and ~13% of the variance in 322 observed  $J_{max25}$  (Fig. S12 b, d) for both temperature response functions. These results suggest 323 324 that our model is able to capture many of the key components of the drivers for  $V_{c,max25}$  and  $J_{max25}$  across the globe both in space as well as in time. The remaining portion of uncertainty that 325 cannot be explained by our LUNA model could be related to variability within the 125 species 326 considered in this study. There are inherent intraspecific variations in leaf traits (Valladares et 327 al., 2000) and in photosynthetic capacity (Moran et al., 2015). Data availability limited the 328 number of species that can be considered and favored a universal LUNA model as separate 329 species normally did not cover a sufficiently large range of environmental conditions. Yet, we 330 should be able to fit our model to specific PFTs when additional data become available with a 331 332 large enough coverage of environmental conditions. We expect that such a model would be able to describe and capture adequately a larger portion of the variability observed in  $V_{c,max25}$  and 333 334  $J_{max25.}$ 

Unexplored nutrient limitations and other plant physiological properties could also play a
factor in the limitation of our model. For example, the nitrogen use efficiency of tropical plants
(typically modest to low nitrogen) can be diminished by low phosphorus (Cernusak et al., 2010;
Reich and Oleksyn, 2004), suggesting that our model could be improved by considering multiple

nutrient limitations (Goll et al., 2012; Walker et al., 2014; Wang et al., 2010). Our treatment of
photosynthetic capacity could also be improved by incorporating species-specific mesophyll and
stomatal conductance (Medlyn et al., 2011), by analyzing leaf properties such as leaf life span
(Wright et al., 2004), or by considering soil nutrient, soil water availability, and soil pH (Maire
et al., 2015).

344 Another potential reason why the model is unable to explain a significant part of uncertainty in the observation is due to that fact that the measurement error on  $V_{c,max25}$  and  $J_{max25}$  is rarely 345 reported in the literature. Measurement errors on  $V_{c,max25}$  and  $J_{max25}$  could result from many 346 347 sources. Firstly, through different statistical fitting approaches used to fit the Farquhar et al. model (Dubois et al., 2007; Manter and Kerrigan, 2004) to determine the transition  $C_i$  value (the 348 value of C<sub>i</sub> used to differentiate between Rubisco and RUBP limitations), which are not yet 349 consistent in the literature (Miao et al., 2009). Secondly, obtaining accurate or biologically 350 realistic estimates of dark respiration is often challenging (but see Dubois et al., 2007), and as 351 such, dark respiration is sometimes not reported (Medlyn et al., 2002b). 352

353

# 354 4.2. Importance of environmental control on $V_{c,max25}$ and $J_{max25}$

Our model predicts that higher temperatures generally lead to lower values of  $V_{c,max25}$  and J<sub>max25</sub> (Fig. 3a, c). As temperature increases, the nitrogen use efficiencies of  $V_{c,max}$  and J<sub>max</sub> also increase and thus plants need a lower amount of nitrogen allocated for carboxylation and electron transport. This is true for all the sites except for  $V_{c,max25}$  in the hotter regions when TRF2 was used (Fig. S9a). The reason is because LUNA model will use a higher increase in night-time temperature (e.g., 22 to 30°C) than daytime temperature (e.g., from 31 to 33°C) , because the daytime temperature is constrained by the maximum temperature for optimization in TRF2 (i.e., 362 33°C). To maximize the net photosynthetic carbon gain, the model predicts a higher proportion 363 of nitrogen allocated to carboxylation to compensate for a higher nighttime respiration rate. 364 Therefore, the LUNA model predicts a higher value of  $V_{c,max25}$ . Yet, this may result from the 365 deficiency of TRF2 by not considering thermal acclimation under future global warming 366 (Lombardozzi et al., 2015).

367 Our model predicts that  $CO_2$  has negligible effects on  $J_{max25}$ , which is supported by reports from other studies (e.g. Maroco et al., 2002). A meta-analysis of 12 FACE experiments indicated 368 reductions of  $J_{max}$  of approximately 5% but a 10% reduction in  $V_{c,max25}$  under elevated CO<sub>2</sub> (Long 369 370 et al., 2004). Our model also predicts that relative humidity has little effect on  $V_{c,max25}$ . This may be due to the fact that most of the values of  $V_{c,max25}$  and  $J_{max25}$  used in our dataset were reported 371 with relatively high humidity values; however, our model may have underestimated the effects of 372 prolonged drought on  $V_{c,max25}$  under low humidity conditions (Xu and Baldocchi, 2003), which 373 we did not consider. Under prolonged drought, plants close their stomata and photosynthesis is 374 greatly reduced (Breshears et al., 2008; McDowell, 2011). Without carbon input and high 375 temperatures during drought, photosynthetic enzymes may degenerate, which could decrease 376  $V_{c,max25}$  substantially (Limousin et al., 2010; Xu and Baldocchi, 2003). 377

There are many different ways to incorporate environmental controls on  $V_{c,max25}$  and  $J_{max25}$ . One simple approach is to use empirical statistical models between environmental variables and  $V_{c,max25}$  and  $J_{max25}$  (e.g. Ali et al., 2015; Verheijen et al., 2013), which has been shown to improve the model simulations (Verheijen et al., 2015). One key limitation of such models is that they may have risk of inaccurate extrapolation under novel future climate conditions. The optimization model such as LUNA could be more reliable in their predictions under novel future climate conditions as they account for the key assumptions that could be robust under different 385 environmental conditions. By far, optimality approaches have been used to predict many different plant structures and functions under different environmental conditions such as carbon 386 allocations (Franklin et al., 2012), leaf C:N (Thomas and Williams, 2014), root distribution 387 (McMurtrie et al., 2012), and stomata conductance (Cowan and Farquhar, 1977). For the 388 photosynthetic capacity optimization, Haxeltine and Prentice (1996) has used an optimization 389 approach to predict  $V_{c,max25}$  based on the trade-off between photosynthesis and respiration, which 390 has been incorporated into land surface models including LPJ-GUESS (Smith et al., 2001) and 391 LPJmL (Sitch et al., 2003). Both LUNA model and the model of Haxeltine and Prentice (1996) 392 393 considered the  $V_{c,max25}$  component and respiration; however, LUNA model is currently only designed for the leaf level while model of Haxeltine and Prentice (1996) is applicable for both 394 the leaf and canopy level. The key improvements of LUNA model include the explicit 395 considerations of other important processes such as light capture and electron transport and 2) 396 the evaluations against global datasets under different environmental conditions. 397

398

### 399 4.3. Importance of changes in $V_{c,max25}$ and $J_{max25}$ to future photosynthesis estimation

Our model suggests that most regions of the world will likely have reductions in  $V_{c,max25}$  (Fig. 4b 400 and Fig. S8b), because increased temperature (Fig. S13) coupled with elevated CO<sub>2</sub> will increase 401 nitrogen use efficiency of Rubisco and thus plants are able to reduce the amount of nitrogen 402 allocated for Rubisco to reduce the carbon cost required for enzyme maintenance. Similarly, 403  $J_{max25}$  will also decrease globally, except in regions where the present growing temperatures are 404 high (Fig. S12b). The increase of  $J_{max25}$  can be attributed to leaf temperature limitation and 405 increased shortwave radiation (Fig. S14 and S15). Temperature will have a small impact on 406 407 nitrogen allocation in regions with historically high growing season temperatures because leaf temperature in already close to or high than the upper limit of optimal nitrogen allocation (42°C
for TRF1 and 33°C for TRF2). Based on eq. (A11), higher levels of shortwave solar radiation
will increase nitrogen allocation to electron transport (Evans and Poorter, 2001).

If we do not account for the potential acclimation of  $V_{c,max25}$  and  $V_{c,max25}$  under future climate 411 conditions as predicted by the LUNA model, our analysis indicates that ESM predictions of 412 future global photosynthesis at the uppermost leaf layer will likely be overestimated by as much 413 as 10-16% if  $V_{c,max25}$  and  $J_{max25}$  are held fixed (Fig. 7). The higher overestimation for TRF2 414 (16.3%) than TRF1 (10.1%) could result from the fact that TFR2 does not account for future 415 416 thermal acclimation and thus the LUNA model predicts a large nitrogen allocation acclimation for future climate change. In both cases, our results suggest that, to reliably predict global plant 417 responses to future climate change, ESMs should incorporate models that use environmental 418 control on  $V_{c,max25}$  and  $J_{max25}$ . It has been recently suggested that nitrogen-related factors are not 419 well represented in ESMs (Houlton et al., 2015; Wieder et al., 2015). Our nitrogen partitioning 420 scheme would help alleviate biases into the predictions of future photosynthetic rates, and also 421 climate processes that are dependent on these predictions (Bonan et al., 2011; Knorr and Kattge, 422 2005; Rogers, 2014). 423

424

#### 425 **5.** Code availability

This LUNA model has been implemented into CLM5.0 which will be openly available afterits release in early 2016. Meanwhile, we have codes available in the form of MATLAB,

FORTRAN and C#. They can be obtained upon request by sending an email to <u>cxu@lanl.gov</u>.

429

# 430 6. Appendices

# 431 Appendix A: Leaf Utilization of Nitrogen for Assimilation (LUNA) Model

The LUNA model (Xu et al., 2012) considers nitrogen allocation within a given leaf layer in the canopy that has a predefined leaf-area-based plant leaf nitrogen availability (LNC<sub>a</sub>; gN/m<sup>2</sup> leaf) to support its growth and maintenance. The structure of the LUNA model is adapted from Xu et al. (2012), where the plant nitrogen at the leaf level is divided into four pools: structural nitrogen ( $N_{str}$ ; g N/m<sup>2</sup> leaf), photosynthetic nitrogen ( $N_{psn}$ ; g N/m<sup>2</sup> leaf), storage nitrogen ( $N_{store}$ ; g N/m<sup>2</sup> leaf), and respiratory nitrogen ( $N_{resp}$ ; g N/m<sup>2</sup> leaf). Namely,

438 
$$LNC_a = N_{psn} + N_{str} + N_{store} + N_{resp}.$$
 (A1)

The photosynthetic nitrogen,  $N_{psn}$ , is further divided into nitrogen for light capture ( $N_{lc}$ ;  $g N/m^2$ leaf), nitrogen for electron transport ( $N_{et}$ ;  $g N/m^2$  leaf), and nitrogen for carboxylation ( $N_{cb}$ ; g $N/m^2$  leaf). Namely,

442 
$$N_{psn} = N_{et} + N_{cb} + N_{lc}.$$
 (A2)

443 The structural nitrogen,  $N_{str}$ , is calculated as the multiplication of leaf mass per unit area (LMA: 444 g biomass/m<sup>2</sup> leaf), and the structural nitrogen content (SNC: g N/g biomass). Namely,

445 
$$N_{str} = \text{SNC} \cdot \text{LMA},$$
 (A3)

where SNC is set to be fixed at 0.002 (gN/g biomass), based on data on C:N ratio from dead wood (White et al., 2000). The functional leaf nitrogen content (FNC<sub>a</sub>; gN/m<sup>2</sup> leaf) is defined by subtracting structural nitrogen content,  $N_{str}$ , from the total leaf nitrogen content (LNC<sub>a</sub>; gN/m<sup>2</sup> leaf),

$$FNC_a = LNC_a - N_{str}.$$
 (A4)

451 We assume that plants optimize their nitrogen allocations (i.e.,  $N_{store}$ ,  $N_{resp}$ ,  $N_{lc}$ ,  $N_{et}$ ,  $N_{cb}$ ) to 452 maximize the net photosynthetic carbon gain, defined as the gross photosynthesis (*A*) minus the 453 maintenance respiration for photosynthetic enzymes ( $R_{psn}$ ), under specific environmental 454 conditions and given plant's strategy of leaf nitrogen use. Namely, the solutions of nitrogen 455 allocations {  $N_{store}$ ,  $N_{resp}$ ,  $N_{lc}$ ,  $N_{et}$ ,  $N_{cb}$  } can be estimated as follows,

· · •

456 
$$\{\hat{N}_{store}, \hat{N}_{resp}, \hat{N}_{lc}, \hat{N}_{et}, \hat{N}_{cb}\} = \underset{N_{store}+N_{lc}+N_{at}+N_{cb}< FNC_{a}}{argmax} (A-R_{psn}).$$
 (A5)

The gross photosynthesis, A, was calculated with a coupled leaf gas exchange model based on the Farquhar et al. (1980) model of photosynthesis and Ball-Berry-type stomatal conductance model (Ball et al., 1987) (See Appendix C for details). The maintenance respiration for photosynthetic enzymes,  $R_{psn}$ , is calculated by the multiplication of total photosynthetic nitrogen (N<sub>psn</sub>) and the maintenance respiration cost for photosynthetic enzyme ( $NUE_{rp}$ , see Appendix D). Namely,

$$R_{psn} = NUE_{rp}N_{psn}.$$
 (A6)

In the LUNA model, the maximum electron transport rate ( $J_{max}$ ;  $\mu$ mol electron m<sup>-2</sup> s<sup>-1</sup>) is simulated to have a baseline allocation of nitrogen and additional nitrogen allocation to change depending on the average daytime photosynthetic active radiation (PAR;  $\mu$ mol electron m<sup>-2</sup> s<sup>-1</sup>), day length (hours) and air humidity. Specifically, we have

468 
$$J_{max} = J_{max0} + J_{maxb1}f(day \, length)f(humidity)\alpha \, PAR.$$
(A7)

469 The baseline electron transport rate,  $J_{max0}$ , is calculated as follows,

$$470 J_{max0} = J_{maxb0} FNC_a NUE_{J_{max}} (A8)$$

471 where  $J_{maxb0}$  (unitless) is the baseline proportion of nitrogen allocated for electron transport rate. 472  $NUE_{Jmax}(\mu \text{mol electron s}^{-1} \text{g}^{-1}\text{N})$  is the nitrogen use efficiency of  $J_{max}$  (see eq. (D2) for details). 473  $J_{maxb1}$  (unitless) is a coefficient determining the response of the electron transport rate to amount 474 of absorbed light (*i.e.*,  $\alpha PAR$ ). f(day length) is a function specifies the impact of day length 475 (hours) on  $J_{max}$  in view that longer day length has been demonstrated by previous studies to 476 alter  $V_{c,max25}$  and  $J_{max25}$  (Bauerle et al., 2012; Comstock and Ehleringer, 1986) through 477 photoperiod sensing and regulation (e.g. Song et al., 2013). Following Bauerle et al. (2012), 478  $f(day \, length)$  is simulated as follows,

479 
$$f(day \, length) = \left(\frac{day \, length}{12}\right)^2$$
. (A9)

*f*(*humidity*) represents the impact of air humitidy on  $J_{max}$ . We assume that higher humidity leads to higher  $J_{max}$  with less water limitation on stomta opening and that low relative humidity has a stronger impact on nitrogen allocation due to greater water limitation. When relative humidity (RH; unitless) is too low, we assume that plants are physiologically unable to reallocate nitrogen. We therefore assume that there exists a critical value of relative humidity (RH<sub>0</sub> = 0.25; unitless), below which there is no optimal nitrogen allocation. Based on the above assumptions, we have

487 
$$f(humidity) = \left(1 - e^{\left(-H\frac{\max(RH - RH_0, 0)}{1 - RH_0}\right)}\right),$$
 (A10)

488 where H (unitless) specifies the impact of relative humidity on electron transport rate. Replacing 489 eq. (A7) with eqs. (A 8), (A9) and (A10), we have

490 
$$J_{max} = J_{maxb0} FNC_a NUE_{J_{max}} + J_{maxb1} \left(\frac{day \, length}{12}\right)^2 \left(1 - e^{\left(-H\frac{max(RH-RH_0,0)}{1-RH_0}\right)}\right) \alpha \text{ PAR.} (A11)$$

491 The efficiency of light energy absorption (unitless),  $\alpha$ , is calculated depending on the amount of 492 nitrogen allocated for light capture,  $N_{lc}$ . Following Niinemets and Tenhunen (1997), we have,

493 
$$\alpha = \frac{0.292}{1 + \frac{0.076}{N_{lc}C_b}},$$
 (A12)

where 0.292 is the conversion factor from photon to electron.  $C_b$  is the conversion factor (1.78) from nitrogen to chlorophyll. After we estimate  $J_{max}$ , the actual electron transport rate with the daily maximum radiation ( $J_x$ ) can be calculated using the empirical expression of Smith (1937),

497 
$$J_x = \frac{\alpha PAR_{max}}{\left(1 + \frac{\alpha^2 PAR_{max}^2}{J_{max}^2}\right)^{0.5}},$$
(A13)

where  $PAR_{max}$  (µmol m<sup>-2</sup> s<sup>-1</sup>) is the maximum photosynthetically active radiation during the day. Based on Farquhar et al. (1980) and Wullschleger (1993), we can calculate the electronlimited photosynthetic rate under daily maximum radiation (W<sub>jx</sub>) and the Rubisco-limited photosynthetic rate (W<sub>c</sub>) as follows,

502 
$$W_{J_x} = K_j J_x, \tag{A14}$$

503 
$$W_c = K_c V_{c,max}, \tag{A15}$$

where  $K_j$  and  $K_c$  as the conversion factors for  $J_x$ ,  $V_{c,max}$  ( $V_{c,max}$  to  $W_c$  and  $J_x$  to  $W_{J_x}$ ), respectively [see eqs. (C4) and (C6) in Appendix C for details of calculation]. Based on Xu et al. (2012), Maire et al. (2012) and Walker et al. (2014), we assume that  $W_c$  is proportional to  $W_{J_x}$ . Specifically, we have

508 
$$W_c = t_{c,j} W_{J_x}$$
, (A16)

where  $t_{c,j}$  is the ratio of  $W_c$  to  $W_{J_x}$ . We recognize that this ratio may change depending on the nitrogen use efficiency of carboxylation and electron transport (Ainsworth and Rogers, 2007) and therefore introduce the modification as follows,

512 
$$t_{c,j} = t_{c,j_0} \left( \frac{NUE_c/NUE_j}{NUE_{c0}/NUE_{j0}} \right)^{0.5},$$
 (A17)

where  $t_{c,j_0}$  (unitless) is the ratio of Rubisco limited rate to light limited rate, NUE<sub>c0</sub> (µmol CO<sub>2</sub> s<sup>-1</sup> <sup>1</sup> g<sup>-1</sup>N), NUE<sub>j0</sub> (µmol CO<sub>2</sub> s<sup>-1</sup> g<sup>-1</sup>N) are the daily nitrogen use efficiency of  $W_c$  and  $W_j$  under reference climate conditions defined as the 25°C leaf temperature and atmospheric CO<sub>2</sub> 516 concentration of 380 ppm, with leaf internal CO<sub>2</sub> concentration set as 70% of the atmospheric CO<sub>2</sub> concentration. NUE<sub>c</sub> ( $\mu$ mol CO<sub>2</sub> s<sup>-1</sup> g<sup>-1</sup>N), NUE<sub>i</sub> ( $\mu$ mol CO<sub>2</sub> s<sup>-1</sup> g<sup>-1</sup>N) are the nitrogen use 517 efficiency of  $W_c$  and  $W_j$  at the current climate conditions. See eqs (D6) and (D7) for details of 518 calculation. The term  $\frac{\text{NUE}_{c}/\text{NUE}_{j}}{\text{NUE}_{c0}/\text{NUE}_{j0}}$  determines that the higher nitrogen use efficiency of  $W_c$ 519 compared to that of  $W_i$  will lead to a higher value of  $t_{c,i}$  (or a higher value of  $W_c$  given the same 520 value of  $W_i$ ). The exponent 0.5 was used to ensure that the response of  $V_{c,max}$  to elevated CO<sub>2</sub> is 521 522 down-regulated by approximately 10% when CO<sub>2</sub> increased from 365 ppm to 567 ppm as reported by Ainsworth & Rogers (2007). 523

524 Replacing eq. (A16) with eqs. (A14), (A15) and (A17) , we are able to estimate the 525 maximum carboxylation rate ( $V_{c,max}$ ;  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) as follows,

526 
$$V_{c,max} = t_{c,j_0} \left( \frac{NUE_c/NUE_j}{NUE_{c0}/NUE_{j0}} \right)^{0.5} \left( \frac{K_j}{K_c} \right) J_x.$$
(A18)

527 Following Collatz et al. (1991a), the total respiration ( $R_t$ ) is calculated in proportion to  $V_{c,max}$ ,

528 
$$R_t = 0.015 V_{c,max}$$
. (A19)

Accounting for the daytime and nighttime temperature, we are able to estimate the dailyrespirations as follows,

531 
$$R_{td} = R_t [D_{day} + D_{night} f_r(T_{night}) / f_r(T_{day})], \qquad (A20)$$

where  $D_{day}$  and  $D_{night}$  are daytime and nighttime durations in seconds.  $f_r(T_{night})$  and  $f_r(T_{day})$ are the temperature response functions for respiration (see eq. (B1) for details).

In summary, given an initial estimation of  $N_{lc}$ , we are able to first estimate the efficiency of light energy absorption  $\alpha$  using eq. (A12). With that, we are able to estimate the maximum electron transport rate ,  $J_{max}$ , using eq. (A11). The nitrogen allocated for electron transport can thus be calculated as follows,

538 
$$N_{et} = \frac{J_{max}}{NUE_{Jmax}}.$$
 (A21)

Then, based on eq. (A18), we are able to estimate the corresponding the maximum carboxylation rate  $V_{c,max}$  and the nitrogen allocated for carboxylation as follows,

541 
$$N_{cb} = \frac{V_{c,max}}{NUE_{Vc,max}}$$
(A22)

where  $NUE_{Vc,max}$  is the nitrogen use efficiency for  $V_{c,max}$ . See eq. (D1) for details of calculation. Using eq. (A 20), we are able to estimate  $R_{td}$  and thus the nitrogen allocated for respiration as follows,

545 
$$N_{resp} = \frac{R_{td}}{NUE_r} , \qquad (A23)$$

where  $NUE_r$  is nitrogen use efficiency of enzymes for respiration. See eq. (D3) for details of calculation. Finally, the "storage" nitrogen is calculated as follows,

548 
$$N_{store} = FNC_a - N_{resp} - N_{cb} - N_{lc} - N_{et}.$$
 (A24)

Note that this "storage" nitrogen is mainly a remaining component of  $FNC_a$ . Its formulation is 549 different from the formulation of Xu et al (2012) where  $N_{store}$  is set as a linear function of net 550 photosynthetic rate. This modification is based on the observations that the preliminary fitting to 551 data using the linear function shows no dependence of  $N_{store}$  on net photosynthetic rate. To 552 make the solutions realistic, we set minimum of  $N_{store}$  as 5% of  $NC_a$  in view of potential 553 554 nitrogen for plant functionality that is not accounted for by photosynthesis and respiration. By exploring different values of nitrogen allocated for light capture  $N_{lc}$  and using the eqs. (A21-23), 555 we will find the "optimal" nitrogen allocations ( $\hat{N}_{store}, \hat{N}_{resp}, \hat{N}_{lc}, \hat{N}_{et}, \hat{N}_{cb}$ ) until the net 556 photosynthetic rate is maximized (see eq. (A5)) given a specific set of nitrogen allocation 557 coefficients (i.e.,  $J_{maxb0}$ ,  $J_{maxb1}$ , H, and  $t_{c,j_0}$ ). The detailed optimization algorithms are 558 implemented as follows: 559

| 560 | 1)                                                                                               | Increase the nitrogen allocated $(N_{lc})$ for light capture (from a small initial value of 0.05)      |  |  |  |
|-----|--------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|--|--|--|
| 561 |                                                                                                  | and calculate the corresponding light absorption rate $\alpha$ with eq. (A12);                         |  |  |  |
| 562 | 2)                                                                                               | Calculate $J_{max}$ from eq. (A11) and derive the nitrogen allocated to electron transport, $N_{et}$ , |  |  |  |
| 563 |                                                                                                  | using eq. (A21);                                                                                       |  |  |  |
| 564 | 3)                                                                                               | Calculate $V_{c,max}$ from eq. (A18) and derive the nitrogen allocated to Rubisco, $N_{cb}$ , using    |  |  |  |
| 565 |                                                                                                  | eq. (A22);                                                                                             |  |  |  |
| 566 | 4)                                                                                               | Calculate the total respiration $R_{td}$ from eq. (A20) and derive the nitrogen allocated to           |  |  |  |
| 567 |                                                                                                  | respiration, $N_{resp}$ , using eq. (A23);                                                             |  |  |  |
| 568 | 5)                                                                                               | Calculate the total nitrogen invest in photosynthetic enzymes including nitrogen for                   |  |  |  |
| 569 |                                                                                                  | electron transport, carboxylation and light capture using eq. (A2);                                    |  |  |  |
| 570 | 6)                                                                                               | Calculate the gross photosynthetic rate, A, and the maintenance respiration for                        |  |  |  |
| 571 |                                                                                                  | photosynthetic enzymes, $R_{psn}$ , by eq. (A6);                                                       |  |  |  |
| 572 | 7)                                                                                               | Repeat steps 1) to 6) until the increase from previous time step in A is smaller than or               |  |  |  |
| 573 |                                                                                                  | equal to the increase in $R_{psn.}$                                                                    |  |  |  |
| 574 | Si                                                                                               | nce the response of $V_{c,max}$ and $J_{max}$ to increasing temperature shows a steady rise to an      |  |  |  |
| 575 | optim                                                                                            | um followed by a relatively rapid decline (Bernacchi et al., 2003; Kattge and Knorr, 2007;             |  |  |  |
| 576 | Leuni                                                                                            | ng, 2002; Medlyn et al., 2002a), we postulate that the detrimental heat stress on leaf                 |  |  |  |
| 577 | enzyn                                                                                            | natic activity beyond this optimum (Crafts-Brandner and Law, 2000; Crafts-Brandner and                 |  |  |  |
| 578 | Salvucci, 2000; Law and Crafts-Brandner, 1999; Spreitzer and Salvucci, 2002) will cause the      |                                                                                                        |  |  |  |
| 579 | leaf to fail to optimize its nitrogen allocation. Consequently, we hypothesized that plants only |                                                                                                        |  |  |  |
| 580 | optimize nitrogen allocation up to their optimum enzymatic activity, which is 42°C for TRF1 and  |                                                                                                        |  |  |  |
| 581 | 33°C for TRF2. Regardless of whether plants acclimate to temperature or not, we assume that      |                                                                                                        |  |  |  |
| 582 | they c                                                                                           | lo not optimally allocate nitrogen when leaf temperature is below 5°C because low                      |  |  |  |

temperatures could substantially limit plant enzymes (Martin et al., 1978; Öquist et al., 1980;
Strand and Öquist, 1988).

585 After we get the optimal nitrogen allocations  $(\hat{N}_{store}, \hat{N}_{resp}, \hat{N}_{lc}, \hat{N}_{et}, \hat{N}_{cb})$ , we are able to 586 estimate the  $V_{c,max25}$  and  $J_{max25}$  by rearranging eqs. (A21) and (A22) as follows,

587 
$$V_{c,\max 25} = \hat{N}_{cb} NUE_{Vc,\max 25}$$
 (A25)

588 
$$J_{\max 25} = \hat{N}_{cb} NUE_{Jmax 25}$$
 (A26)

where  $NUE_{Vc,max25}$  and  $NUE_{Jmax25}$  are the nitrogen use efficiency for  $V_{c,max25}$  and  $J_{max25}$ . See eqs. (D1) and (D2) in Appendix D for details of calculations.

#### 592 Appendix B: Temperature response functions

### 593 *Temperature dependence of Rubisco & respiration*

594 The temperature dependence of Rubisco kinetic parameters  $(K_c, K_o, \tau)$  and mitochondrial

respiration in light ( $R_d$ ) (Farquhar et al., 1980) was an Arrhenius function taken from Bernacchi

- et al. (2001). The temperature response functions of Rubisco kinetic parameters used are
- 597 outlined below, which were the same irrespective of whether plants were assumed to acclimate
- to growth temperatures (Temperature response function one; TRF1) or not (Temperature
- response function two; TRF2).

607

600 Community land model version 4.5 (CLM4.5) (Oleson et al., 2013) uses the partial pressures 601 of oxygen, *O* as 20900Pa. The kinetic properties of Rubisco which depend on temperature are 602 Rubisco specific factor,  $\tau$  (Jordan and Ogren, 1984),  $K_{cc}$  and  $K_{o}$ , which are the Michaelis-Menten 603 constants for CO<sub>2</sub> and O<sub>2</sub>, respectively. The temperature response function of  $R_d$  and kinetic 604 properties of Rubisco ( $K_{cc}$ ,  $K_o$ ,  $\tau$ ) are described below, where the fixed coefficients of the 605 equations are values at 25°C.

606 
$$f_r(T_1) = e^{[(46390/RT_0)(1-T_0/T_1)]}$$
 (B1)

608 
$$K_0(T_1) = 27840e^{[(36380/RT_0)(1-T_0/T_1)]}$$
 (B2)

609 
$$K_c(T_1) = 40.49e^{[(79430/RT_0)(1-T_0/T_1)]}$$
 (B3)

610 
$$\tau(T_1) = 2407.834e^{[(37830/RT_0)(1-T_0/T_1)]}$$
 (B4)

- In the above equations, *R* is the universal gas constant (8.314 J mol<sup>-1</sup> K<sup>-1</sup>),  $T_I$  is the leaf
- temperature (*K*) and the reference temperature,  $T_0 = 298.15K$ .

# 613 Temperature dependence of $V_{c,max}$ and $J_{max}$

Temperature sensitivities of  $V_{c,max}$  and  $J_{max}$  were simulated using a modified Arrhenius function (e.g. Kattge and Knorr, 2007; Medlyn et al., 2002a; Walker et al., 2014). Because the temperature relationship could acclimate, we examined Kattge & Knorr (2007)'s formulation of

- 617 with and without temperature acclimation to plant growth temperature. We used two temperature
- 618 dependence functions of  $V_{c,max}$  and  $J_{max}$ , which are described below.
- 619 *Temperature response function one* (TRF1)

Fundamentally, TRF1 is a temperature dependence of  $V_{c,max}$  and  $J_{max}$ , which is based on the formulation and parameterization as in Medlyn et al. (2002a) but further modified by Kattge & Knorr (2007) to make the temperature optima a function of growth temperature ( $T_g$ ; °C).

623 
$$V_{c,max}(T_1, T_g) = V_{c,max25} f_{V_{c,max}}(T_1, T_g)$$
(B5)

624 with

625 
$$f_{V_{c,max}}(T_1, T_g) = \frac{\left(1 + e^{\left[(S_v T_0 - H_d)/(RT_0)\right]}\right) e^{\left[(H_a/RT_0)(1 - T_0/T_1)\right]}}{1 + e^{\left[(S_v T_1 - H_d)/(RT_1)\right]}}$$
(B6)

where  $V_{c,max25}$  is the value of  $V_{c,max}$  at the reference temperature ( $T_0 = 298.15K$ ).  $H_a$  (J mol<sup>-1</sup>) is energy of activation and  $H_d$  (J mol<sup>-1</sup>) is the energy of deactivation. The entropy term,  $S_v$  (J mol<sup>-1</sup>  $K^{-1}$ ), is now a function of temperature (Kattge and Knorr, 2007):  $S_v = a + bT_g$ , where *a* and *b* are acclimation parameters for  $S_v$ , *R* is the universal gas constant (8.314 J mol<sup>-1</sup> K<sup>-1</sup>) and the leaf temperature is  $T_1(K)$ .

TRF1 is implemented in CLM4.5 by Oleson et al. (2013), who uses the form of temperature dependence of  $V_{c,max}$  and  $J_{max}$  as shown in Eq. B5, but with limited temperature acclimation, where  $S_v = 668.39 - 1.07 * min(max(tgrowth, 11), 35)$ . Other parameters that are present in CLM4.5 model include,  $H_a = 72000$  J mol<sup>-1</sup> and  $H_d = 200000$  J mol<sup>-1</sup>. The values of the acclimation parameters (a = 668.39 and b = -1.07) were taken from Table 3 of Kattge & Knorr (2007), which were fixed across our data set. The same values of a and b are used by CLM4.5. A equation similar to eq. (B6),  $f_{J_{max}}(T_1, T_g)$ , is used to describe the temperature dependence of  $J_{max}$  with the corresponding  $S_v$  equation (that considers limited temperature acclimation). The corresponding values of the acclimation parameters (*a* and *b*), were again taken from Table 3 of Kattge & Knorr (2007) and were fixed across our data set. The same values of *a* and *b* are used by CLM4.5. We used the remaining parameter values as in CLM4.5 that included,  $H_a = 50000 \text{ J mol}^{-1}$  and  $H_d = 200000 \text{ J mol}^{-1}$ .

644 *Temperature response function two* (TRF2)

TRF2 does not consider temperature acclimation. The formulation of TRF2 is same as TRF1 except that in TRF2, the entropy term;  $S_v$  (J mol<sup>-1</sup> K<sup>-1</sup>) is fixed across our data set. The values of  $S_v$  were taken from Table 3 of Kattge & Knorr (2007), which were fixed across our data set. For  $V_{c,max25}$ ,  $S_v$  was 649.12 J mol<sup>-1</sup> K<sup>-1</sup>, and for  $J_{max25}$ ,  $S_v$  was 646.22 J mol<sup>-1</sup> K<sup>-1</sup>.

#### 650 Appendix C: The Farquhar Photosynthesis & Ball-Berry model

### 651 *Overview*

Photosynthesis is described using a system of three equations and three unknown variables. 652 The three unknown variables include 1) the net rate of leaf photosynthesis (A); 2) the stomatal 653 conductance  $(g_s)$ ; and 3) the intercellular partial pressure of CO<sub>2</sub> (C<sub>i</sub>). All of the unknown 654 variables influence one another. The three equations include 1) the Farquhar's non-linear 655 equation (A vs  $C_i$ ); 2) the Ball–Berry equation ( $g_s$  vs A); and 3) the diffusion equation ( $A = g_s$  ( $C_a$ 656  $-C_i$ ). We solved all of these equations simultaneously by taking an iterative approach (Collatz 657 et al., 1991a; Harley et al., 1992; Leuning, 1990). The detailed algorithm for modeling 658 photosynthesis is described below. 659

# 660 *Modelling Photosynthesis*

The photosynthetic rate (A) depends upon (*i*) the amount, activity, and kinetic properties of Rubisco, and (*ii*) the rate of ribulose-1,5 bisphosphate (RuBP) regeneration via electron transport (Farquhar et al., 1980). The 'minimum' of these two limiting conditions yields the following expression,

665

$$A = \min(W_c, W_j) \tag{C2}$$

where  $W_c$  is the Rubisco limited rate and  $W_j$  is the electron transport limited rate. The Rubiscolimited carboxylation can be described by,

$$W_c = K_c V_{c,max} , \qquad (C3)$$

669 with

670 
$$K_c = \frac{\max(0, C_i - \frac{0.50}{\tau})}{C_i + K_{cc} (1 + \frac{0}{K_o})}, \qquad (C4)$$

where  $V_{c,max}$  is the maximum rate of carboxylation, competitive with respect to both CO<sub>2</sub> and oxygen, and  $K_{cc}$  and  $K_o$  are Michaelis constants for carboxylation and oxygenation, respectively. 673  $\tau$  is the specificity factor for Rubisco (Jordan and Ogren, 1984), while  $C_i$ , and O are the partial 674 pressures of CO<sub>2</sub> and O<sub>2</sub> in the intercellular air space, respectively. Likewise, the electron-675 limited rate of carboxylation can be expressed by,

$$W_j = K_j J , \qquad (C5)$$

677 with

678 
$$K_j = \frac{\max(0, C_i - \frac{0.50}{\tau})}{4(C_i + 2\frac{0.50}{\tau})},$$
 (C6)

where J is the potential rate of electron transport, and the factor 4 indicates that the transport of four electrons will generate sufficient ATP and NADPH for the regeneration of RuBP in the Calvin cycle (Farquhar and von Caemmerer, 1982). The potential rate of electron transport is dependent upon irradiance, I, according to the empirical expression of Smith (1937),

683 
$$J = \frac{\alpha I}{\left(1 + \frac{\alpha^2 I^2}{Jmax^2}\right)^{1/2}}$$
(C7)

684 where  $\alpha$ , the efficiency of light energy conversion is considered as 0.292 (unitless) (Niinemets 685 and Tenhunen, 1997) and  $J_{max}$  is the maximum rate of electron transport.

686

#### 687 <u>Ball-Berry Model</u>

688 The stomatal conductance (g, m/s) was evaluated by the Ball-Berry empirical stomatal 689 conductance model (Ball et al., 1987):

$$g = g_0 + m \frac{A \operatorname{RH}}{c_a} \tag{C8}$$

where RH is the relative humidity (unitless) at the leaf surface,  $C_a$  is the CO<sub>2</sub> concentration at the leaf surface, and  $g_0$  (0.0005 s/m) and *m* are the maximum stomatal conductance and slope (9, constant across all C<sub>3</sub> species), respectively. The estimation of *A* could be sensitive to the choice of maximum stomatal conductance slope, which we set the same for all species, despite the evidence that this parameter varies both within and across species (Harley and Baldocchi, 1995; Wilson et al., 2001). A recent synthesis provides the first analysis of the global variation in stomatal slope based on an alternative algorithm that considers representation of optimal stomatal behavior (Lin et al., 2015). However, following CLM4.5, which uses the Ball-Berry empirical stomatal conductance model (Ball et al., 1987), we fixed the value of stomatal slope (*m*) as 9 for all PFTs in our study.

701

### 702 Calculation of photosynthesis and stomata conductance

We solved Farquhar's non-linear equation (A vs  $C_i$ ), the Ball-Berry equation ( $g_s$  vs A) and the diffusion equation ( $A = g_s$  ( $C_a - C_i$ ) simultaneously by taking an iterative approach (Collatz et al., 1991a; Harley et al., 1992; Leuning, 1990) until values of A,  $g_s$ , and  $C_i$  were obtained. The three equations were solved in two phases; the first phase included solving the equations for which Rubisco was limiting while the second phase considered light limitation. The following steps were followed:



concentration), the temperature dependence functions of  $V_{c,max}$  and  $J_{max}$  (see Appendix

B), and the temperature dependence of Rubisco kinetics (*O*, *τ*, *K*<sub>c</sub> and *K*<sub>o</sub>, Appendix B), *A*was calculated from equation (C2).

2) CO<sub>2</sub> concentration at the leaf surface  $(C_a)$  was determined by calculating the difference

- between  $C_i$  and the partial pressure due to A, wind speed and the dimension of the leaf.
- 3) Given A and  $C_a$ , and using equation C8, stomatal conductance (g) was determined.

- 4)  $C_i$  was determined by calculating the difference between  $C_a$  and partial pressure due to *A* and boundary conditions of the stomata.
- 5) Using the leaf energy balance based on absorbed short-wave radiation, molar latent heat
- content of water vapor, air temperature, and a parameter that governs the rate of
- convective cooling (38.4 J  $\text{m}^{-2} \text{ s}^{-1} \text{ K}^{-1}$ ) (Jarvis, 1986; Moorcroft et al., 2001), leaf
- 721 temperature was calculated.
- The above five steps were repeated in a systematic way until *g* was equilibrated. The final valueof *A* was then recorded.

# 725 Appendix D: Nitrogen use efficiencies

The nitrogen use efficiency for  $V_{c,max}$  ( $NUE_{V_{c,max}}$ ,  $\mu$ mol CO<sub>2</sub> g<sup>-1</sup> N s<sup>-1</sup>) is estimated from a baseline nitrogen use efficiency 25°C ( $NUE_{V_{c,max}25}$ ) and a corresponding temperature response function at as follows,

729 
$$NUE_{V_{c,\max}} = NUE_{V_{c,\max 25}} \times f_{V_{c,\max}}(T,T_g), \tag{D1}$$

730 with

731 
$$NUE_{V_{c,max25}} = 47.3 \times 6.25$$

where the constant 47.3 is the specific Rubisco activity ( $\mu$ mol CO<sub>2</sub> g<sup>-1</sup> Rubisco s<sup>-1</sup>) measured at 25°C and the constant 6.25 is the nitrogen binding factor for Rubisco (g Rubisco g<sup>-1</sup> N) (Rogers, 2014).  $f_{V_{c,max}}(T,T_g)$  is the function specifying the temperature dependence of  $V_{c,max}$  with T as the leaf temperature () and  $T_g$  as the growth air temperature (See Appendix B for details of the temperature dependence of  $V_{c,max}$ ).

The nitrogen use efficiency for  $J_{max}$  ( $NUE_{J_{max}}$ ,  $\mu$ mol electron g<sup>-1</sup> N s<sup>-1</sup>) is estimated based on a characteristic protein cytochrome *f*(*Evans and Poorter, 2001*),

,

739 
$$NUE_{J_{max}} = NUE_{J_{max}} \times f_{Jmax}(T, T_g), \qquad (D2)$$

740 with

741 
$$NUE_{J_{max25}} = 8.06 \times 156$$

where the coefficient 156 is the maximum electron transport rate for cytochrome *f* at 25°C( $\mu$ mol electron/ $\mu$ mol cytochrome *f*); 8.06 is the nitrogen binding coefficient for cytochrome *f* ( $\mu$ mol cytochrome *f* g<sup>-1</sup> N in bioenergetics).  $f_{Jmax}(T, T_g)$  is a function specifies the dependence of  $J_{max}$ on temperature (See Appendix B for details of the temperature dependence of  $J_{max}$ ).

The nitrogen use efficiency of enzymes for respiration ( $\mu$ mol CO<sub>2</sub> g<sup>-1</sup>N day<sup>-1</sup>), *NUE<sub>r</sub>*, is assumed to be temperature-dependent. Specifically, it is calculated as follows,

748 
$$NUE_r = 33.69 \left[ D_{day} f_r(T_{day}) + D_{night} f_r(T_{night}) \right]$$
(D3)

where 33.69 is the specific nitrogen use efficiency for respiration at 25°C ( $\mu$ mol CO<sub>2</sub> g<sup>-1</sup> N s<sup>-1</sup>) (Makino and Osmond, 1991) and  $f_r(T)$  specifies the dependence of respiration on temperature.  $D_{day}$  and  $D_{night}$  is the daytime and nighttime length in seconds.

The maintenance respiration cost for all photosynthetic enzymes ( $NUE_{rp}$ ,  $\mu$ mol CO<sub>2</sub> g<sup>-1</sup>N s<sup>-1</sup>) is calculated as follows:

754 
$$NUE_{rp} = NUE_{rp25}f_r(T,T_g), \tag{D4}$$

where  $NUE_{rp25}$  is the nitrogen use efficiency at 25 °C.  $NUE_{rp25}$  is estimated from the observation of  $J_{max25}$  and  $V_{c,max25}$  as follows,

757 
$$NUE_{rp25} = \frac{0.8 \times 0.5 \times 0.015 \times V_{c,\max 25}}{\frac{J_{\max 25}}{NUE_{J_{\max 25}}} + \frac{V_{c,\max 25}}{NUE_{V_{c,\max 25}}} + 0.2},$$
(D5)

where the total respiration is set as 1.5% of  $V_{c,\max}$  (Collatz et al., 1991b). We assume that 50% of the total respiration is used for maintenance respiration (Van Oijen et al., 2010) and 80% of the maintenance respiration is used for photosynthetic enzyme. In view that the light absorption rate is generally around 80% (Evans and Poorter, 2001), we set the nitrogen for light capture as 0.2 based on eq. (A12) in Appendix A.  $NUE_{J_{max25}}$  and  $NUE_{V_{c,max25}}$  are the nitrogen use efficiency for  $J_{max25}$  and  $V_{c,max25}$  estimated from eqs. (D1) and (D2). In this study, we used the estimated mean value of 0.715 for  $NUE_{rp25}$  based on the data of Ali *et al.* (2015).

The nitrogen use efficiency for carboxylation ( $NUE_c$ ) is calculated as the multiplication of conversion factor  $K_c$  and the nitrogen use efficiency for  $V_{c,max}$  follows:

767 
$$NUE_c = K_c. NUE_{V_{c,max}},$$
 (D6)

where  $K_c$  is calculated based on the actual internal CO<sub>2</sub> concentrations and leaf temperature (see eq. (C4) for details). Correspondingly, the reference nitrogen use efficiency for carboxylation (NUE<sub>c0</sub>) is calculated using the eq. (D5) except that  $K_c$  is calculated based on the reference internal CO<sub>2</sub> concentration of 26.95 Pa and the reference leaf temperature of 25°C. The reference internal CO<sub>2</sub> concentration is estimated by assuming 70% of the atmospheric CO<sub>2</sub> concentration of 380 ppm and an air pressure of 101, 325 Pa.

The nitrogen use efficiency for electron transport ( $NUE_j$ ) is calculated as the multiplication of conversion factor  $K_j$  and the nitrogen use efficiency for  $J_{max}$  follows:

$$NUE_j = K_j. NUE_{J_{max}}, \tag{D7}$$

where  $K_j$  is calculated based on the actual internal CO<sub>2</sub> concentrations and leaf temperature (see eq. (C6) in Appendix C for details). Correspondingly, the reference nitrogen use efficiency for electron transport (*NUE<sub>j0</sub>*) is calculated using the eq. (D6) except that  $K_j$  is calculated based on the reference internal CO<sub>2</sub> concentration of 26.95 Pa and the reference leaf temperature of 25°C. The reference internal CO<sub>2</sub> concentration is estimated by assuming 70% of the atmospheric CO<sub>2</sub>
concentration of 380 ppm and an air pressure of 101, 325 Pa.

# 783 7. Acknowledgements

This work is funded by UC Lab Research Program (ID: 2012UCLRP0IT00000068990) and

by the DOE Office of Science, Next Generation Ecosystem Experiment (NGEE) programs in the

arctic and in the tropics. This submission is under public release with the approved LA-UR-14-

787 23309.

### 789 **8. References**

- Ainsworth, E. A. and Rogers, A.: The response of photosynthesis and stomatal conductance to rising (CO<sub>2</sub>): mechanisms and environmental interactions, Plant Cell Environment, 30, 258-270, 2007.
- Ali, A. A., Xu, C., Rogers, A., McDowell, N. G., Medlyn, B. E., Fisher, R. A., Wullschleger, S. D., Reich, P. B.,
- 793 Vrugt, J. A., Bauerle, W. L., Santiago, L. S., and Wilson, C. J.: Global scale environmental control of plant
- 794 photosynthetic capacity, Ecological Applications, doi: 10.1890/14-2111.1, 2015. 2015.
- Ball, J. T., Woodrow, I. E., and Berry, J. A.: A model predicting stomatal conductance and its contribution
  to the control of photosynthesis under different environmental conditions., Dordrecht, The
  Netherlands1987, 221-224.
- Bauerle, W. L., Oren, R., Way, D. A., Qian, S. S., Stoy, P. C., Thornton, P. E., Bowden, J. D., Hoffman, F. M.,
- and Reynolds, R. F.: Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling, PNAS, 109, 8612-8617, 2012.
- 801 Bernacchi, C. J., Pimentel, C., and Long, S. P.: *In vivo* temperature response functions of parameters 802 required to model RuBP-limited photosynthesis, Plant, Cell & Environment, 26, 1419-1430, 2003.
- 803 Bernacchi, C. J., Singsaas, E. L., Pimentel, C., Portis JR, A. R., and Long, S. P.: Improved temperature
- response functions for models of Rubisco-limited photosynthesis, Plant, Cell & Environment, 24, 253-259, 2001.
- 806 Block, K. and Mauritsen, T.: Forcing and feedback in the MPI-ESM-LR coupled model under abruptly 807 quadrupled CO<sub>2</sub>, Journal of Advances in Modeling Earth Systems, 5, 676-691, 2013.
- Bonan, G. B., Lawrence, P. J., Oleson, K. W., Levis, S., Jung, M., Reichstein, M., Lawrence, D. M., and
  Swenson, S. C.: Improving canopy processes in the community land model version 4 (CLM4) using global
  flux fields empirically inferred from FLUXNET data, Journal of Geophysical Research, 116, 1-22, 2011.
- Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M., and Oelson, K. W.: A dynamic global vegetation model
- for use with climate models: concepts and description of simulated vegetation dynamics, Global Change
- 813 Biology, 9, 1543-1566, 2003.
- 814 Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D., McDowell, N. G., and
- 815 Pockman, W. T.: Tree die-off in response to global change-type drought: mortality insights from a
- decade of plant water potential measurements, Frontiers in Ecology and the Environment, 7, 185-189,2008.
- 818 Canadell, J. G., Le Quéré, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T. J., Gillett,
- 819 N. P., Houghton, R. A., and Marland, G.: Contributions to accelerating atmospheric CO2 growth from 820 economic activity, carbon intensity, and efficiency of natural sinks, Proceedings of the National Academy
- 820 economic activity, carbon intensity, and efficien821 of Sciences, 104, 18866-18870, 2007.
- 822 Cernusak, L. A., Winter, K., and Turner, B. L.: Leaf nitrogen to phosphorus ratios of tropical trees:
- experimental assessment of physiological and environmental controls, New Phytologist, 185, 770-779, 2010.
- 825 Collatz, G. J., Ball, J. T., Grivet, C., and Berry, J. A.: Physiological and environmental regualtion of stomatal 826 conductance, photosynthesis, and transpiration: A model that includes a laminar boundary layer,
- Agricultural and Forest Meteorology, 54, 107-136, 1991a.
- Collatz, G. J., Ball, J. T., Grivet, C., and Berry, J. A.: Physiological and environmental regulation of stomatal
  conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer,
  Agricultural and Forest Meteorology, 54, 107-136, 1991b.
- 831 Comstock, J. and Ehleringer, J. R.: Photoperiod and photosynthetic capacity in *Lotus scoparius* Plant, Cell
  832 & Environment, 9, 609-612, 1986.
- Cowan, I. and Farquhar, G.: Stomatal function in relation to leaf metabolism and environment, 1977,
  471-505.

- Crafts-Brandner, S. J. and Law, R. D.: Effect of heat stress on the inhibition and recovery of ribulose-1,5bisphosphate carboxylase/oxygenase activation state Planta, 212, 67-74, 2000.
- 837 Crafts-Brandner, S. J. and Salvucci, M. E.: Rubisco activase constrains the photosynthetic potential of 838 leaves at high temperature and CO<sub>2</sub>, PNAS, 97, 2000.
- Base Dewar, R. C.: Maximum entropy production and plant optimization theories, Philosophical Transactions
  of the Royal Society B, 365, 1429-1435, 2010.
- 841 Dubois, J.-J. B., Fiscus, E. L., Booker, F. L., Flowers, M. D., and Reid, C. D.: Optimizing the statistical
- 842 estimation of the parameters of the Farguhar–von Caemmerer–Berry model of photosynthesis, New
- 843 Phytologist, 176, 402-414, 2007.
- Evans, J. R. and Poorter, H.: Photosynthetic acclimation of plants to growth irradiance: the relative
  importance of specific leaf area and nitrogen partitioning in maximizing carbon gain, Plant, Cell &
  Environment, 24, 755-767, 2001.
- Farquhar, G. D. and von Caemmerer, S. (Eds.): Modelling of photosynthetic response to environmental
  conditions, Heidelberg-Berlin-New York: Springer-Verlag, 1982.
- Farquhar, G. D., Von Caemmerer, S., and Berry, J.: A biochemical model of photosynthetic  $CO_2$ assimilation in leaves of  $C_3$  species, Planta, 149, 78-90, 1980.
- 851 Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, Å., and Dybzinski,
- 852 R.: Modeling carbon allocation in trees: a search for principles, Tree Physiology, 32, 648-666, 2012.
- 853 Friedlingstein, P., Meinshausen, M., Arora, V. K., Jones, C. D., Anav, A., Liddicoat, S. K., and Knutti, R.:
- Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks, Journal of Climate, 27, 511-526, 2014.
- Friend, A.: Use of a model of photosynthesis and leaf microenvironment to predict optimal stomatal conductance and leaf nitrogen partitioning, Plant, Cell & Environment, 14, 895-905, 1991.
- Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., van Bodegom, P. M., and
  Niinemets, U.: Nutrient limitation reduces land carbon uptake in simulations with a model of combined
  carbon, nitrogen and phosphorus cycling, Biogeosciences, 9, 3547-3569, 2012.
- Hanson, P. J., Amthor, J. S., Wullschleger, S. D., Wilson, K. B., Grant, R. F., Hartley, A., Hui, D., Hunt, J. E.
- 862 R., Johnson, D. W., Kimball, J. S., King, A. W., Luo, Y., McNulty, S. G., Sun, G., Thornton, P. E., Wang, S.,
- Williams, M., Baldocchi, D. D., and Cushman, R. M.: OAK FOREST CARBON AND WATER SIMULATIONS:
   MODEL INTERCOMPARISONS AND EVALUATIONS AGAINST INDEPENDENT DATA, Ecological Monographs,
- 865 74, 443-489, 2004.
- Harley, P. C. and Baldocchi, D. D.: Scaling carbon dioxide and water vapour exchange from leaf to canopy
  in a decisuous forest. I. Leaf model parametrization, Plant, Cell & Environment, 18, 1146-1156, 1995.
- Harley, P. C., Thomas, R. B., Reynolds, J. F., and Strain, B. R.: Modelling photosynthesis of cotton grown
  in elevated CO<sub>2</sub> Plant, Cell & Environment, 15, 271-282, 1992.
- Haxeltine, A. and Prentice, I. C.: A general model for the light-use efficiency of primary production,
  Functional Eocolgy, 10, 551-561, 1996.
- Houlton, B. Z., Marklein, A. R., and Bai, E.: Representation of nitrogen in climate change forecasts,
  Nature Clim. Change, 5, 398-401, 2015.
- Hurrell, J. W., Holland, M. M., Gent, P. R., Ghan, S., Kay, J. E., Kushner, P. J., Lamarque, J. F., Large, W. G.,
- 875 Lawrence, D., Lindsay, K., Lipscomb, W. H., Long, M. C., Mahowald, N., Marsh, D. R., Neale, R. B., Rasch,
- P., Vavrus, S., Vertenstein, M., Bader, D., Collins, W. D., Hack, J. J., Kiehl, J., and Marshall, S.: The
- 877 Community Earth System Model: A Framework for Collaborative Research, Bulletin of the American
- 878 Meteorological Society, 94, 1339-1360, 2013.
- Jarvis, P. G.: Coupling of carbon and water interactions in forest stands, Tree Physiology, 2, 347-368,1986.

- Jordan, D. B. and Ogren, W. L.: The CO<sub>2</sub>/O<sub>2</sub> specificity of ribulose 1,5-biphosphate
   carboxylase/oxygenase. Dependence on ribulose-biphosphate concentration, pH and temperature,
   Planta, 161, 308-313, 1984.
- 884 Kattge, J. and Knorr, W.: Temperature acclimation in a biochemical model of photosynthesis: a 885 reanalysis of data from 36 species, Plant, Cell & Environment, 30, 1176-1190, 2007.
- 886 Kattge, J., Knorr, W., Raddatz, T., and Wirth, C.: Quantifying photosynthetic capacity and its relationship
- to leaf nitrogen content for global-scale terrestrial biosphere models, Global Change Biology, 15, 976-991, 2009.
- Knorr, W. and Kattge, J.: Inversion of terrestrial ecosystem model parameter values against eddy
   covariance measurements by Monte Carlo sampling, Global Change Biology, 11, 1333-1351, 2005.
- Laloy, E. and Vrugt, J. A.: High-dimensional posterior exploration of hydroligic models using multiple-try DREAM(<sub>zs</sub>) and high-performance computing, Water Resources Research, 48, W01526, 2012.
- Law, R. D. and Crafts-Brandner, S. J.: Inhibition and acclimation of photosynthesis to heat stress is closely
- correlated with activation of ribulose-1,5-bisphosphate carboxylase/ oxygenase, Plant Physiology, 120,
  173-181, 1999.
- Leuning, R.: Modeling stomatal behavior and photosynthesis of *Eucalyptus grandis*, Australian Journal of
   Plant Physiology, 17, 159-175, 1990.
- Leuning, R.: Scaling to a common temperature improves the correlation between photosynthesis parameters J<sub>max</sub> and V<sub>cmax</sub>, Journal of Experimental Botany, 307, 345-347, 1997.
- Leuning, R.: Temperature dependence of two parameters in a photosynthesis model, Plant, Cell &Environment, 25, 1205-1210, 2002.
- Limousin, J.-M., Misson, L., Lavoir, A.-V., Martin, N. K., and Rambal, S.: Do photosynthetic limitations of
   evergreen Quercus ilex leaves change with long-term increased drought severity?, Plant, Cell &
- 904 Environment, 33, 863-875, 2010.
- Lin, Y.-S., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S., Eamus, D., de Dios, V. R., Mitchell, P., Ellsworth, D. S., de Beeck, M. O., Wallin, G., Uddling, J., Tarvainen, L., Linderson, M.-L.,
- 907 Cernusak, L. A., Nippert, J. B., Ocheltree, T. W., Tissue, D. T., Martin-StPaul, N. K., Rogers, A., Warren, J.
- 908 M., De Angelis, P., Hikosaka, K., Han, Q., Onoda, Y., Gimeno, T. E., Barton, C. V. M., Bennie, J., Bonal, D.,
- 909 Bosc, A., Low, M., Macinins-Ng, C., Rey, A., Rowland, L., Setterfield, S. A., Tausz-Posch, S., Zaragoza-
- 910 Castells, J., Broadmeadow, M. S. J., Drake, J. E., Freeman, M., Ghannoum, O., Hutley, L. B., Kelly, J. W.,
- 911 Kikuzawa, K., Kolari, P., Koyama, K., Limousin, J.-M., Meir, P., Lola da Costa, A. C., Mikkelsen, T. N.,
- Salinas, N., Sun, W., and Wingate, L.: Optimal stomatal behaviour around the world, Nature Clim.Change, advance online publication, 2015.
- 914 Lombardozzi, D. L., Bonan, G. B., Smith, N. G., Dukes, J. S., and Fisher, R. A.: Temperature acclimation of
- 915 photosynthesis and respiration: A key uncertainty in the carbon cycle-climate feedback, Geophysical
  916 Research Letters, 42, 8624-8631, 2015.
- Long, S. P., Ainsworth, E. A., Rogers, A., and Ort, D. R.: Rising atmospheric carbon dioxide: plants FACE
  the future, Ann. Rev. Plant. Biol, 55, 591-628, 2004.
- Maire, V., Martre, P., Kattge, J., Gastal, F., Esser, G., Fontaine, S., and Soussana, F.: The coordination of leaf photosynthesis links C and N fluxes in C<sub>3</sub> plant species, PLos ONE, 7, e38245, 2012.
- 921 Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K.,
- 922 Ellsworth, D., Niinemets, Ü., Ordonez, A., Reich, P. B., and Santiago, L. S.: Global effects of soil and 923 climate on leaf photosynthetic traits and rates, Global Ecology and Biogeography, 24, 706-717, 2015.
- 924 Makino, A. and Osmond, B.: Effects of nitrogen nutrition on nitrogen partitioning between chloroplasts
- and mitochondria in pea and wheat, Plant Physiology, 96, 355-362, 1991.
- 926 Manter, D. K. and Kerrigan, J.: A/C<sub>i</sub> curve analysis across a range of woody plant speices: influence of
- 927 regression analysis parameters and mesophyll conductance, Journal of Experimental Botany, 55, 2581-
- 928 2588, 2004.

- Maroco, J. P., Breia, E., Faria, T., Pereira, J. S., and Chaves, M. M.: Effects of long-term exposure to elevated CO<sub>2</sub> and N fertilization on the development of photosynthetic capacity and biomass accumulation in *Quercus suber* L., Plant, Cell & Environment, 25, 105-113, 2002.
- Martin, B., Martensson, O., and Öquist, G.: Seasonal effects on photosynthetic electron transport and
  fluorescence properties in isolated chloroplasts of *Pinus sylvestris*, Physiologia Plantarum, 44, 102-109,
  1978.
- 935 Mayer, D. G. and Butler, D. G.: Statistical validation, Ecological Modelling, 68, 21-32, 1993.
- 936 McDowell, N.: Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality, 937 Plant Physiology, 155, 1051-1059 2011.
- 938 McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, D. A., and Norby, R. J.:
- Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging, Ecology
   and Evolution, 2, 1235-1250, 2012.
- 941 Medlyn, B. E., Badeck, F.-W., De Pury, D. G. G., Barton, C. V. M., Broadmeadow, M., Ceulemans, R., De
- 942 Angelis, P., Forstreuter, M., Jach, M. E., Kellomäki, S., Laitat, E., Marek, M., Philippot, S., Rey, A.,
- 943 Strassemeyer, J., Laitinen, K., Liozon, R., Portier, B., Proberntz, P., Wang, K., and Jarvis, P. G.: Effects of
- 944 elevated [CO<sub>2</sub>] on photosynthesis in European forest species: a meta-analysis of model parameters,
  945 Plant, Cell & Environment, 22, 1475-1495, 1999.
- 946 Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., Le Roux, X.,
- 947 Montpied, P., Strassemeyer, J., Walcroft, A., Wang, K., and Loustau, D.: Temperature response of
- parameters of a biochemically based model of photosynthesis. II. A review of experimental data, Plant
- 949 Cell Environment, 25, 1167-1179, 2002a.
- Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. A., Prentice, I. C., Barton, C. V. M., Crous, K. Y., De
   Angelis, P., Freeman, M., and Wingate, L.: Reconciling the optimal and empirical approaches to
   modelling stomatal conductance, Global Change Biology, 10, 1365-2486, 2011.
- Medlyn, B. E., Loustau, D., and Delzon, S.: Temperature response of parameters of a biochemically based
   model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Ait.), Plant, Cell &
   Environment, 25, 1155-1165, 2002b.
- Medlyn, B. E., Robinson, B. A., Clement, R., and McMurtrie, R. E.: On the validation of models of forest
   CO<sub>2</sub> exchange using eddy covariance data: some perils and pitfalls, Tree Physiology, 25, 839-857, 2005.
- Meehl, G. A., Boer, G. J., Covey, C., Latif, M., and Stouffer, R. J.: The Coupled Model Intercomparison
  Project (CMIP), Bulletin of the American Meteorological Society, 81, 313-318, 2000.
- Miao, Z., Xu, M., Lathrop, R. G., and Wang, Y.: Comparison of the A–Cc curve fitting methods in
  determining maximum ribulose 1.5-bisphosphate carboxylase/oxygenase carboxylation rate, potential
  light saturated electron transport rate and leaf dark respiration, Plant, Cell & Environment, 32, 109-122,
  2009.
- 964 Moorcroft, P. R., Hurtt, G. C., and Pacala, S. W.: A method for scaling vegetation dynamics: the 965 ecosystem demography model (ED), Ecological Monographs, 71, 557-586, 2001.
- 966 Moran, E. V., Hartig, F., and Bell, D. M.: Intraspecific trait variation across scales: implications for 967 understanding global change responses, Global Change Biology, doi: 10.1111/gcb.13000, 2015. n/a-n/a,
- 968 2015.
- Niinemets, Ü. and Tenhunen, J. D.: A model separating leaf structural and biphysiological effects on
  carbon gain along light gradients for the shade-tolerant species *Acer saccharum*, Plant, Cell &
  Environment, 20, 845-866, 1997.
- 972 Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, S., Li, F., Riley,
- 973 W. J., Subin, Z. M., Swenson, S. C., Thornton, P. E., Bozbiyik, A., Fisher, R., Kluzek, E., Lamarque, J.-F.,
- 274 Lawrence, P. J., Leung, L. R., Lipscomb, W., Muszala, S., Ricciuto, D. M., Sacks, W., Sun, Y., Tang, J., and
- 975 Yang, Z.-L.: Technical Description of version 4.5 of the Community Land Model (CLM). NCAR Technical
- 976 Note NCAR/TN-503+STR, National Center for Atmospheric Research, Boulder, CO, 2013.

- 977 Öquist, G., Brunes, L., Hällgren, J.-E., Gezelius, K., Hallén, M., and Malmberg, G.: Effects of artificial frost 978 hardening and winter stress on net photosynthesis, photosynthetic electron transport and RuBP 979 carboxylase activity in seedlings of *Pinus sylvestris*, Physiologia Plantarum, 48, 526-531, 1980.
- 980 Prentice, I. C., Dong, N., Gleason, S. M., Maire, V., and Wright, I. J.: Balancing the costs of carbon gain
- 981 and water transport: testing a new theoretical framework for plant functional ecology, Ecology Letters, 982 17, 82-91, 2014.
- 983 Raddatz, T., Reick, C., Knorr, W., Kattge, J., Roeckner, E., Schnur, R., Schnitzler, K. G., Wetzel, R. G., and 984 Jungclaus, J.: Will the tropical land biosphere dominate the climate-carbon cycle feedback during the 985 twenty-first century?, Climate Dynamics, 29, 565-574, 2007.
- 986 Reich, P. B., Kloeppel, B. D., Ellsworth, D., and Walters, M. B.: Different photosynthesis nitorgen relations 987 in decidious hardwood and evergreen coniferous tree species Oecologia, 104, 24-30, 1995.
- 988 Reich, P. B. and Oleksyn, J.: Global patterns of plant leaf N and P in relation to temperature and latitude, 989 PNAS, 101, 11001-11006, 2004.
- 990 Reich, P. B., Walters, M. B., Tjoelker, M. G., Vanderklein, D., and Buschena, C.: Photosynthesis and 991 respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree 992 species differing in relative growth rate, Functional Ecology, 12, 395-405, 1998.
- 993 Riebeek, H.: The Carbon Cycle, NASA Earth Observatory, 994 http://earthobservatory.nasa.gov/Features/CarbonCycle/, 2011.
- 995 Ripullone, F., Grassi, G., Lauteri, M., and Borghetti, M.: Photosynthesis-nitrogen relationships: 996 interpretation of different patterns between Pseudotsuga menziesii and Populus x euroamericana in a 997 mini-stand experiment, Tree Physiology, 23, 137-144, 2003.
- Rogers, A.: The use and misuse of V<sub>c,max</sub> in earth system models, Photosynthesis Research, 119, 1-15, 998 999 2014.
- 1000 Ryan, M. G.: Foliar maintenance respiration of subalpine and boral trees and shrubs in relation to 1001 nitrogen concentration, Plant, Cell & Environment, 18, 765-772, 1995.
- 1002 Schaefer, K., Schwalm, C. R., Williams, C., Arain, M. A., Barr, A., Chen, J. M., Davis, K. J., Dimitrov, D., 1003 Hilton, T. W., Hollinger, D. Y., Humphreys, E., Poulter, B., Raczka, B. M., Richardson, A. D., Sahoo, A.,
- 1004 Thornton, P., Vargas, R., Verbeeck, H., Anderson, R., Baker, I., Black, T. A., Bolstad, P., Chen, J., Curtis, P. 1005
- S., Desai, A. R., Dietze, M., Dragoni, D., Gough, C., Grant, R. F., Gu, L., Jain, A., Kucharik, C., Law, B., Liu, 1006 S., Lokipitiya, E., Margolis, H. A., Matamala, R., McCaughey, J. H., Monson, R., Munger, J. W., Oechel, W., 1007 Peng, C., Price, D. T., Ricciuto, D., Riley, W. J., Roulet, N., Tian, H., Tonitto, C., Torn, M., Weng, E., and
- 1008 Zhou, X.: A model-data comparison of gross primary productivity: Results from the North American
- Carbon Program site synthesis, Journal of Geophysical Research: Biogeosciences, 117, G03010, 2012. 1009
- Schymanski, S. J., Sivapalan, M., Roderick, M. L., Hutley, L. B., and Beringer, J.: An optimality-based 1010 1011 model of the dynamic feedbacks between natural vegetation and the water balance, Water Resources 1012 Research, 45, W01412, 2009.
- 1013 Sellers, P. J., Dickinson, R., Randall, D. A., Betts, A. K., Hall, F. G., Berry, J. A., Collatz, G. J., Denning, A. S., 1014 Mooney, H. A., Nobre, A. D., Sato, N., Field, C. B., and HendersonSellers, A.: Modeling the exchanges of 1015 energy, water, and carbon between continents and the atmosphere, Science, 275, 502-509, 1997.
- 1016
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., 1017 Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and 1018 terrestrail carbon cycling in the LPJ dynamic global vegetation model, Global Change Biology, 9, 161-185, 1019 2003.
- 1020 Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of 1021 terrestrial ecosystems: comparing two contrasting approaches within European climate space, Global
- 1022 Ecology and Biogeography, 10, 621-637, 2001.
- 1023 Smith, E.: The influence of light and carbon dioxide on photosynthesis, General Physiology, 20, 807-830, 1024 1937.

- Song, Y. H., Ito, S., and Imaizumi, T.: Flowering time regulation: photoperiod- and temperature-sensing
  in leaves, Trends in Plant Science, 18, 575-583, 2013.
- 1027 Spreitzer, R. J. and Salvucci, M. E.: Rubisco: structure, regulatory interactions, and possibilities for a 1028 better enzyme, Annual Review of Plant Biology, 53, 449-475, 2002.
- 1029 Strand, M. and Öquist, G.: Effects of frost hardening, dehardening and freezing trees on in vivo
- 1030 fluorescence of seedlings of Scots pine (*Pinus sylvestris* L.), Plant, Cell & Environment, 11, 231-238, 1988.
- 1031 Taylor, K. E., Stouffer, R. J., and Meehl, G. A.: An overview of CMIP5 and the experiment design, Bulletin
- 1032 of the American Meteorological Society, 93, 485-498, 2013.
- Thomas, R. Q. and Williams, M.: A model using marginal efficiency of investment to analyze carbon and
  nitrogen interactions in terrestrial ecosystems (ACONITE Version 1), Geosci. Model Dev., 7, 2015-2037,
  2014.
- Valladares, F., Wright, S. J., Lasso, E., Kitajima, K., and Pearcy, R. W.: PLASTIC PHENOTYPIC RESPONSE TO
   LIGHT OF 16 CONGENERIC SHRUBS FROM A PANAMANIAN RAINFOREST, Ecology, 81, 1925-1936, 2000.
- 1038 Van Oijen, M., Schapendonk, A., and Hoglind, M.: On the relative magnitudes of photosynthesis, 1039 respiration, growth and carbon storage in vegetation, Ann Bot-London, 105, 793-797, 2010.
- 1040 Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C., Kattge, J., and van
  1041 Bodegom, P. M.: Inclusion of ecologically based trait variation in plant functional types reduces the
  1042 projected land carbon sink in an earth system model, Global Change Biology, 21, 3074-3086, 2015.
- 1043 Verheijen, L. M., Brovkin, V., Aerts, R., Bönisch, G., Cornelissen, J. H. C., Kattge, J., Reich, P. B., Wright, I.
  1044 J., and van Bodegom, P. M.: Impacts of trait variation through observed trait–climate relationships on
  1045 performance of an Earth system model: a conceptual analysis, Biogeosciences, 10, 5497-5515, 2013.
- Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C.,
  Wohlfahrt, G., Wullschleger, S. D., and Woodward, F. I.: The relationship of leaf photosynthetic traits –
  Vcmax and Jmax to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and
  modeling study, Ecology and Evolution, 4, 3218-3235, 2014.
- 1050 Wang, Y. P., Law, R. M., and Pak, B.: A global model of carbon, nitrogen and phosphorus cycles for the 1051 terrestrial biosphere, Biogeosciences, 7, 2261-2282, 2010.
- 1052 White, M. A., Thornton, P. E., Running, S. W., and Nemani, R. R.: Parameterization and sensitivity 1053 analysis of the BIOME-BCG terrestrial ecosystem model: net primary production controls, Earth 1054 Interactions, 4, 1-85, 2000.
- Whitley, R. J., Catriona, M. O., Macinnis-Ng, C., Hutley, L. B., Beringer, J., Zeppel, M., Williams, M.,
  Taylor, D., and Eamus, D.: Is productivity of mesic savannas light limited or water limited? Results of a
  simulation study, Global Change Biology, 17, 3130-3149, 2011.
- 1058 Wieder, W. R., Cleveland, C. C., Lawrence, D. M., and Bonan, G. B.: Effects of model structural 1059 uncertainty on carbon cycle projections: biological nitrogen fixation as a case study Environmental 1060 Research Letters, 10, 044016, 2015.
- Wilson, K. B., Baldocchi, D. D., and Hanson, P. J.: Leaf age affects the seasonal pattern of photosynthetic
  capacity and net ecosystem exchange of carbon in a deciduous forest, Plant, Cell & Environment, 24,
  571-583, 2001.
- 1064 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin,
- 1065 T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont,
- 1066 B. B., Lee, T. D., Lee, W., Lusk, C. H., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Olesksyn, J., Osada, N.,
- Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J.,
  and Villar, R.: The worldwide leaf economics spectrum, Nature, 428, 821-827, 2004.
- 1069 Wullschleger, S. D.: Biochemical limitations to carbon assimilation in  $C_3$  plants: a retrospective analysis of 1070  $A/C_i$  curves from 109 species, Journal of Experimental Botany 44, 907-920, 1993.
- 1071 Xu, C., Fisher, R., Wullschleger, S. D., Wilson, C. J., Cai, M., and McDowell, N.: Toward a mechanistic
- 1072 modeling of nitrogen limitation on vegetation dynamics, PLos ONE, 7, e37914, 2012.

1073 Xu, L. and Baldocchi, D. D.: Seasonal trends in photosynthetic parameters and stomatal conductance of

- 1074 blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature, Tree Physiology,
  1075 23, 865-877, 2003.
- 1076 Yamori, W., Suzuki, K., Noguchi, K. O., Nakai, M., and Terashima, I.: Effects of Rubisco kinetics and
- 1077 Rubisco activation state on the temperature dependence of the photosynthetic rate in spinach leaves
- 1078 from contrasting growth temperatures, Plant, Cell & Environment, 29, 1659-1670, 2006.

1079

1080

1082 9. Tables

**Table 1** Mean values of parameters obtained by using the Differential Evolution Adaptive
 1083 Metropolis Snooker updater (DREAM-ZS) sampling technique when TRF1 and TRF2 were 1084 1085 used. TRF1 was a temperature response function that considered the potential for acclimation to growth temperature while TRF2 was a temperature response function that did not consider 1086 change in temperature response coefficients to growth temperature. The parameters include; 1087  $J_{maxb0}$  (unitless) - baseline proportion of nitrogen allocated for electron transport rate,  $J_{maxb1}$ 1088 (unitless) - electron transport rate response to light availability,  $t_{c,i0}$  (unitless) – baseline ratio of 1089 Rubisco limited rate to light limited rate, and H (unitless) - electron transport rate response to 1090 relative humidity. The standard deviations are shown in the parentheses. 1091

|      | Statistics | J <sub>maxb0</sub> | $J_{maxb1}$     | t <sub>c,j0</sub> | Н               |
|------|------------|--------------------|-----------------|-------------------|-----------------|
|      | TRF1       | 0.0311 (0.0004)    | 0.1745 (0.0002) | 0.8054 (0.0015)   | 6.0999 (0.2416) |
|      | TRF2       | 0.0322 (0.0002)    | 0.1695 (0.0006) | 0.7760 (0.0031)   | 5.7139 (0.0354) |
| 1093 |            |                    |                 |                   |                 |
| 1094 |            |                    |                 |                   |                 |
| 1095 |            |                    |                 |                   |                 |
| 1096 |            |                    |                 |                   |                 |
| 1097 |            |                    |                 |                   |                 |
| 1098 |            |                    |                 |                   |                 |
| 1099 |            |                    |                 |                   |                 |
| 1100 |            |                    |                 |                   |                 |
| 1101 |            |                    |                 |                   |                 |

1102 **10. Figures** 

#### 1103 **Figure captions**

Figure 1 Percentage of variations ( $r^2$ , ME; model efficiency) in observed  $V_{c,max25}$  ( $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> 1104 s<sup>-1</sup>) explained by modeled  $V_{c max^{25}}$  (a, c) and in observed  $J_{max^{25}}$  (µmol electron m<sup>-2</sup> s<sup>-1</sup>) explained 1105 by modeled  $J_{max25}$  (b, d) across all of the species, using TRF1 (a, b) and TRF2 (c, d), where the 1106 1107 nitrogen allocation model, the environmental variables, leaf mass per leaf area, and the leaf nitrogen contents were used. TRF1 was a temperature response function that considered the 1108 potential for acclimation to growth temperature while TRF2 was a temperature response function 1109 that did not consider change in temperature response coefficients to growth temperature. The  $r^2$  is 1110 derived by a linear regression between observed and modeled values. The dashed line is the 1:1 1111 1112 line.

Figure 2 Effects of changes in nitrogen allocation parameters on the predicted  $V_{c.max25}$  (µmol 1113  $CO_2 \text{ m}^{-2} \text{ s}^{-1}$ ) (a, c) and  $J_{max25}$  (µmol electron m<sup>-2</sup> s<sup>-1</sup>) (b, d). Each parameter ( $J_{maxb0}, J_{maxb1}, t_{c,i0}$ , and 1114 H) was varied one at a time by +/-15% of its value by using either TRF1 (a, b) or TRF2 (c, d). 1115 1116 TRF1 was a temperature response function that considered the potential for acclimation to 1117 growth temperature while TRF2 was a temperature response function that did not consider change in temperature response coefficients to growth temperature. The environmental variables 1118 (day length; 14 hours, daytime radiation; 182 W m<sup>-2</sup>, temperature; 14°C, relative humidity; 0.6 1119 (unitless), and carbon dioxide; 393 ppm) were held fixed. Firstly,  $V_{c,max25}$  and  $J_{max25}$  values were 1120 obtained at changed parameter value. Next, percentage changes in  $V_{c,max25}$  and  $J_{max25}$  were 1121 1122 calculated relative to the baseline values of  $V_{c,max25}$  and  $J_{max25}$ .

1124 Figure 3 Effects of environmental variables (day length, daytime radiation, temperature, relative humidity, and carbon dioxide) on predicted  $V_{c,max25}$  (µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) (a, c) and  $J_{max25}$  (µmol 1125 electron  $m^{-2} s^{-1}$ ) (b, d). Each environmental variable (day length; 14 hours, daytime radiation; 1126 182 W m<sup>-2</sup>, temperature; 14°C, relative humidity; 0.6 (unitless), and carbon dioxide; 393 ppm) 1127 was varied one at a time by +/-15%. TRF1 (a, b) and TRF2 (c, d) were used, with the parameters 1128  $(J_{maxb0}, J_{maxb1}, t_{c,i0}, \text{ and } H)$  being held fixed. TRF1 was a temperature response function that 1129 considered the potential for acclimation to growth temperature while TRF2 was a temperature 1130 1131 response function that did not consider change in temperature response coefficients to growth temperature. Firstly,  $V_{c,max25}$  and  $J_{max25}$  values were obtained at changed environmental 1132 condition. Next, percentage changes in  $V_{c,max25}$  and  $J_{max25}$  were calculated relative to the baseline 1133 values of  $V_{c,max25}$  and  $J_{max25}$ . 1134

1135

Figure 4 Summer season photosynthetic capacity for the top leaf layer in the canopy ( $V_{c,max25}$ ; 1136  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (a),  $J_{max25}$ ;  $\mu$ mol electron m<sup>-2</sup> s<sup>-1</sup> (c)) under historical climatic conditions and the 1137 difference in either  $V_{c,max25}$  (b) or  $J_{max25}$  (d) due to changed climatic conditions. Difference in the 1138 photosynthetic capacity was calculated as that under future climate minus that under historical 1139 climate. Ten-year monthly averages of climatic conditions for the past (1995 - 2004) and the 1140 1141 future (2090-2099) were used to drive the model. The model was run by using TRF1, which was a temperature response function that considered the potential for acclimation to growth 1142 temperature. 1143

**Figure 5** Sensitivity of  $V_{c,max25}$  ( $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) to changes in environmental variables (a; Temperature, b; Radiation, c; Humidity, and d; CO<sub>2</sub>) at the global scale by using TRF1. TRF1

1147 was a temperature response function that considered the potential for acclimation to growth 1148 temperature. The sensitivity analysis is conducted by changing the value of individual 1149 environmental variable using 10-year monthly averages of climatic conditions for the past (1995-1150 2004) versus the future (2090-2099) for each individual grid across the globe.

1151

**Figure 6** Sensitivity of  $J_{max25}$  ( $\mu$ mol electron m<sup>-2</sup> s<sup>-1</sup>) to changes in environmental variables (a; Temperature, b; Radiation, c; Humidity, and d; CO<sub>2</sub>) at the global scale using TRF1. TRF1 was a temperature response function that considered the potential for acclimation to growth temperature. The sensitivity analysis is conducted by changing the value of individual environmental variable using 10-year monthly averages of climatic conditions for the past (1995-2004) versus the future (2090-2099) for each individual grid across the globe.

1158

Figure 7 Percentage differences in  $A_{net}$  (µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) for using  $V_{c,max25}$  (µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) 1159 and  $J_{max^{25}}$  (µmol electron m<sup>-2</sup> s<sup>-1</sup>) based on historical climate and that using  $V_{cmax^{25}}$  and  $J_{max^{25}}$ 1160 based on future climate conditions. TRF1 (a) and TRF2 (b) were used in the model simulations. 1161 TRF1 was a temperature response function that considered the potential for acclimation to 1162 growth temperature while TRF2 was a temperature response function that did not consider 1163 change in temperature response coefficients to growth temperature. 10-year monthly averages of 1164 climatic conditions for the past (1995 - 2004) and the future (2090-2099) were used to drive the 1165 model. 1166

1167























#### 





