Global scale environmental control of plant photosynthetic capacity

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Abstract

Photosynthetic capacity, determined by light harvesting and carboxylation reactions, is a key plant trait that determines the rate of photosynthesis; however, in Earth System Models (ESMs) at a reference temperature it is either a fixed value for a given plant functional type or derived from a linear function of leaf nitrogen content. In this study, we conducted a comprehensive analysis that considered correlations of environmental factors with photosynthetic capacity as determined by maximum carboxylation rate scaled to 25°C [i.e., $V_{c,max25}$ (μmol CO_2 m^{-2} s^{-1})] and maximum electron transport rate scaled to 25°C [i.e., J_{max25} (μmol electron m^{-2} s^{-1})] at the global scale. Our results showed that the percentages of variations in observed $V_{c,max25}$ and J_{max25} explained jointly by the environmental factors (i.e. day length, radiation, temperature and humidity) were 2-2.5 times and 6-9 times of that explained by area-based leaf nitrogen content, respectively. Environmental factors influenced photosynthetic capacity mainly through the photosynthetic nitrogen use efficiency, rather than through leaf nitrogen content. The combination of leaf nitrogen content and environmental factors was able to explain ~56% and ~66% of the variation in $V_{c,max25}$ and J_{max25} at the global scale, respectively. Our analyses suggest that model projections of plant photosynthetic capacity and hence land-atmosphere exchange under changing climatic conditions could be substantially improved if environmental factors are incorporated into algorithms used to parameterize photosynthetic capacity in ESMs.

Keywords: climate variables, Earth System Models, and plant traits

Introduction

Our planet is experiencing the warmest temperatures in at least 2000 years (Booth et al. 2012, Friedlingstein et al. 2014) and sophisticated Earth System Models (ESMs) have been developed to simulate the trajectory of climate warming in the coming decades (Meehl et al. 2013, Taylor et al. 2013). A major component of ESMs is the land surface where photosynthesis and respiration drive carbon fluxes between plants and the atmosphere (e.g. Sitch et al. 2003, Oleson et al. 2013). Canopy photosynthetic uptake of CO_2 is a key process in these models, which depends on the environmental conditions (e.g., temperature, radiation and humidity) and the plant's photosynthetic capacity at a reference temperature generally at 25°C. For most of the photosynthesis models within ESMs, photosynthetic capacity is represented by the leaf-level maximum carboxylation rate at 25°C ($V_{c,max25}$, µmol CO_2 m^{-2} s^{-1}) and the leaf-level maximum electron transport rate at 25°C (J_{max25}, µmol electron m^{-2} s^{-1}) (Farquhar et al. 1980, Baldocchi and Meyers 1998, Canadell et al. 2000, Zaehle et al. 2005, Friend 2010, Bonan et al. 2011, Rogers 2014).

Vegetation is represented in ESMs as plant functional types (PFTs) (White et al. 2000, Bonan et al. 2003, Sitch et al. 2003, Oleson et al. 2013), which are parameterized with traits that describe the form and function of a given PFT. $V_{c,max25}$ and J_{max25} of PFTs are either a fixed trait, or, where nitrogen dynamics are simulated, a function of the prognostic leaf nitrogen content (Haxeltine and Prentice 1996, Bonan et al. 2003, Kattge et al. 2009, Thornton et al. 2009, Zaehle et al. 2010). Many empirical studies have shown that $V_{c,max25}$ and J_{max25} correlate with leaf nitrogen content (e.g.Ryan 1995, Reich et al. 1998, Medlyn et al. 1999, Kattge et al. 2009, Rogers 2014) and this relationship forms the basis of many ESM estimations of $V_{c,max25}$ (Kattge et al. 2009, Rogers 2014) and J_{max25} (Kattge and Knorr 2007). Variation in $V_{c,max25}$ and J_{max25} is substantial (Wullschleger 1993, Medlyn et al. 1999) and occurs with growth conditions (Reich et al. 1998, Cai et al. 2007), season (Wilson et al. 2000, Onoda et al. 2005) and among species (Wohlfahrt et al. 1999, Joel et al. 2001, Ellsworth et al. 2004). In view of these large variations, it is well recognized that current ESM parameterization of $V_{c,max25}$ and and J_{max25} over-simplifies the representation of this model input and that refined representation of variables that control $V_{c,max25}$ and J_{max25} are critical for improving model simulations of land-atmosphere carbon exchange (Bonan et al. 2011, Bauerle et al. 2012, Rogers 2014). $V_{c,max25}$ and J_{max25} are tightly coupled, and therefore a fixed ratio of $J_{max25}/V_{c,max25}$ is typically assumed in large modeling schemes but only $V_{c,max25}$ has been measured and studied more extensively (Wullschleger 1993, Leuning 1997, Kattge and Knorr 2007).

Many studies have explored the environmental control of photosynthetic capacity (von Caemmerer and Farquhar 1984, Evans and Poorter 2001, Wilson et al. 2001, Ainsworth and Long 2005, Misson et al. 2006, Bauerle et al. 2012, Maire et al. 2012, Xu et al. 2012). However, they generally consider one or two environmental factors (e.g. CO_2, radiation) or are limited to a specific region or continent. As far as we know, only one study has evaluated the multi-environmental control of photosynthetic capacity at the global scale (Reich et al. 2007); however, that study had key limitations. It did not consider important environmental factors such as day length (Bauerle et al. 2012), nor did it consider radiation levels at different canopy locations (Meir et al. 2002, Niinemets et al. 2007). Most importantly, they focused on light saturated photosynthetic rate (i.e., A_{max}) but not on $V_{c,max25}$ nor on J_{max25}. A_{max} is not a good measure of photosynthetic capacity in view that $V_{c,max25}$ and J_{max25}, and other physiological properties such as stomatal conductance combined with environmental conditions are used to determine A_{max}. Thus, A_{max} is generally not used in ESMs as a parameter of photosynthetic capacity. Furthermore, Reich et al.'s study predicted photosynthetic capacity at a global scale by using annual climate conditions. Long-term averages of climatic conditions (Reich et al. 2007) may not represent the conditions (such as peak growing season) that most influence the achieved rates of photosynthetic capacity. Given that we cannot account for very short-term fluctuations (both due to lack of day-to-day observations and a lack of theory about short-term variation in photosynthetic capacity), in this study, we focus on the intermediate time scale (monthly). In agreement with the half-life time of Rubisco at seven days (Suzuki et al. 2001), we assume that photosynthetic capacity varies with the monthly mean environmental conditions during plant growth (Medlyn et al. 2002a, Kattge and Knorr 2007, Maire et al. 2012).

In order to identify environmental factors that could be incorporated in ESMs to predict photosynthetic capacity (i.e., $V_{c,max25}$ and J_{max25}), we assembled data that included variation in plant growth conditions resulting from seasonal cycles, latitudinal gradients, and different canopy locations and then conducted a comprehensive analysis of photosynthetic capacity across the globe using monthly-mean environmental conditions that include temperature, radiation, humidity, and day length. Environmental factors could potentially affect $V_{c,max25}$ or J_{max25} in many ways including the mass-based leaf nitrogen content (Maire et al. 2012), the specific leaf area (Poorter and Evans 1998), leaf age (Escudero and Mediavilla 2003), and the nitrogen allocation through photosynthetic apparatus and specific activity of photosynthetic enzymes (Poorter and Evans 1998). In this study, we define $V_{c,max25}$ as the product of $NUE_{c,max25}$ (µmol CO_2 $g^{-1}N$ s^{-1}) and area-based leaf nitrogen content (LNC_a; gN m^{-2}), where $NUE_{c,max25}$ is the $V_{c,max25}$ per unit of leaf nitrogen. Similarly, we define J_{max25} as the product of $NUE_{j,max25}$ (µmol electron $g^{-1}N$ s^{-1}) and LNC_a, where $NUE_{j,max25}$ is the J_{max25} per unit of leaf nitrogen and is denoted as a measure of nitrogen-use efficiency of J_{max25}. Based on the above definitions, environmental factors could affect $V_{c,max25}$ or J_{max25} through two pathways, either by modifying the absolute nitrogen content, or by modifying the photosynthetic nitrogen use efficiency. We explored the relative importance of these two pathways to better understand how environmental factors affect $V_{c,max25}$ and J_{max25}.

Methodology

Overview

We obtained individual values of $V_{c,max}$, J_{max} and area-based leaf nitrogen content by digitizing data from the literature. The values of $V_{c,max}$ and J_{max} were first standardized to common kinetic parameters and photosynthetic functions and then scaled to 25°C using a reference temperature response function. The corresponding mean monthly temperature, incident radiation, day length and relative humidity at the time of the measurements were then obtained from the CRUNCEP.v4 dataset (Mitchell and Jones 2005). We assume that at the short-term time scales (e.g., daily basis), photosynthetic rates changes due to environmental conditions (Reich et al. 1991a, Sullivan et al. 1996, Porté and Loustau 1998) but not much on the photosynthetic capacities as determined by $V_{c,max25}$ and J_{max25} (e.g. Xu and Baldocchi 2003). In contrast, at the intermediate time scales (e.g, monthly basis), $V_{c,max25}$ or J_{max25} could change due to plant acclimations to environmental conditions (Meir et al. 2002, Medlyn et al. 2002b, Kattge and Knorr 2007). Therefore, in this study, we used the monthly mean data to investigate how much environmental variables and leaf nitrogen content could contribute to variations in observed $V_{c,max25}$ and J_{max25} using a linear mixed-effects model.

Data and observations

We conducted a literature search on Google Scholar to locate publications that included the key words "$V_{c,max}$" or "J_{max}" and also contained "leaf nitrogen content" or "maximum carboxylation capacity" or "maximum electron transport rate". We identified several more publications from the references cited in these studies. Some of the dataset used in our study are deposited in the global data base of plant traits via the TRY initiative (Kattge et al. 2011). To ensure that our literature review was comprehensive, we also searched the bibliographic resources from Curtis (1996), Wullschleger (1993) and Ainsworth & Rogers (2007), and included the studies that met our basic requirements. We identified a lack of data from the Arctic region and therefore incorporated unpublished data from Alistair Rogers (Brookhaven National Laboratory, NY, USA) collected in Barrow, Alaska as part of the Department of Energy's Next Generation Experiment in the Arctic (NGEE-Arctic). We want to point out that different data sets are used for the analyses of $V_{c,max25}$ and J_{max25} because not all the studies report both $V_{c,max25}$ and J_{max25}.

The $V_{c,max}$ and J_{max} values were standardized to 25°C using reference temperature dependence functions so that a comparison across data could be made at a common temperature. We recognize that this is a highly non-trivial task and that a number of formulations have been made to choose among. Some of these temperature functions show weaker correspondence with the experimental data (Harley and Baldocchi 1995) while other temperature functions do not provide accurate modeled temperature responses of Rubisco-limited photosynthetic rate (McMurtrie and Wang 1993). To ensure that our conclusions are not dependent on the choice of temperature response function (TRF), we explored four alternative functions. The first temperature response function (TRF1) had temperature dependence of Rubisco kinetic parameters and temperature sensitivity of $V_{c,max}$ based on the Q_{10} concept (Collatz et al. 1991, Sellers et al. 1996). The second temperature response function (TRF2) had temperature dependence of Rubisco kinetic parameters (K_c, K_o, τ) based on an Arrhenius function taken from Bernacchi et al. (2001) with the temperature sensitivity of $V_{c,max}$ using an Arrhenius function as in Leuning (2002). The kinetic properties of Rubisco that depend on temperature include Rubisco specific factor (τ) (Jordan and Ogren 1984), and the Michaelis-Menten constants for CO_2 (K_c) and O_2 (K_o). Since relationships of kinetic parameters could acclimate to variation in growth temperature (Yamori et al. 2005, Yamori et al. 2006), the third temperature response function (TRF3) considered Kattge & Knorr (2007)'s formulation of acclimation, where temperature optimum was a function of growth temperature. Finally, the fourth temperature response function (TRF4) was taken from Kattge & Knorr (2007)'s formulation but had limited temperature acclimation, where the plant's growth temperature was constrained between 11°C and 35°C (see Appendix G for details). Exemplary response of $V_{c,max}/V_{c,max25}$ to temperature for all TRFs is presented in Figure 1. To save space, we only included the figures for TRF4 in the main text and placed the figures for other TRFs in the Appendix A. The reason we focus on TRF4 is that it has medium level of temperature acclimation and is currently utilized in one of the ESMs e.g. Community Land Model (CLM4.5) (Oleson et al. 2013).

In this study, we have data for 127 species from a total of 58 studies on $V_{c,max}$, including six studies that specifically considered seasonal cycles of $V_{c,max}$ (see Table A1 for details). We have 636 data points of J_{max} values, which were reported by fifty studies. Studies which reported $V_{c,max}$ or J_{max} over four or more consecutive months were considered as seasonal studies, while the remaining studies were classified as non-seasonal (Table A1 for details). Ten of the non-seasonal studies explored relationships with light attenuation through the canopy profile (Table A1 for details) and were classified as vertical canopy layer studies. In our study, we have a total of 833 data points that encompass $V_{c,max25}$ under different leaf nitrogen contents and environmental conditions.

We used freely available digitization and data extraction software (Engauge Digitizer 5.1: http://digitizer.sourceforge.net) to extract data from figures for a number of studies when they were not reported in text or tables. If the climate covariates (temperatures, radiation and/or specific humidity) were not reported, they were extracted from the CRUNCEP.v4 dataset with a resolution of half a degree (Mitchell and Jones 2005). Specifically, the climate covariates were obtained every six hours within a day using the latitudes, longitudes and the year in which the photosynthesis measurements were made for each study based on a bilinear interpolation. Bilinear interpolation is used to estimate the climate conditions of each study site from the gridded climate data. We assumed that species experienced the mean monthly environmental conditions when photosynthetic measurements were made, instead of using mean annual climatic conditions (Wright et al. 2004, Reich et al. 2007). We expect that monthly summaries of environmental conditions would potentially characterize plant growth conditions better than annual means in view that photosynthetic capacity responses to changing environment due to enzyme turnover (estimated between one to seven days) (Holaday et al. 1992, Piques et al. 2009, Suzuki et al. 2010). Leaf temperatures were usually reported, but plant growth temperature was rarely given. Because we needed the radiation conditions, if the study reported the canopy location (i.e they provided the canopy profile) and hence radiation levels, we used all of the data. For studies that did not report the canopy locations explicitly, we only used the upper 25% of the $V_{c,max}$ and J_{max} data, in view that higher $V_{c,max25}$ and J_{max25} are generally associated with higher canopy locations (Niinemets 1997) and our climate data from CRUNCEP.v4 dataset is only for the top of the canopy.

Specific humidity was used to calculate the relative humidity and vapor pressure deficit using the saturated water vapor pressure equation. The saturated vapor pressure and its derivative, as a function of temperature, were calculated from the eighth-order polynomials fits of Flatau et al. (1992). In this study, we do not consider atmospheric CO_2 concentration as one of the environmental variables because we only have a limited number of species for elevated CO_2 studies (Medlyn et al. 1999, Ainsworth and Rogers 2007), which could lead to potential bias of the CO_2 impact in the analysis given the large amount of variations in $V_{c,max25}$ and J_{max25} across different species.

We did not consider row crops in this study because agricultural practices could confound analysis of the relationships we were exploring. In this work, we focus on C_3 species only because they comprise the bulk of plant species on earth. We acknowledge that leaf life span has been shown to be an important correlate of plant traits such as leaf nitrogen content and photosynthesis per unit leaf mass (Wright et al. 2004). We did not consider leaf lifespan because only a handful number of studies reported its values and therefore we posit that leaf life span is still poorly quantified (but see Reich et al. 2014); however, we do consider evergreen vs. deciduous habit which does account for variation in leaf life-span, albeit in a crude fashion. Our database covers latitudes from -45.5° S to 71.5° N and longitudes -157.2° W to 176.3° E. Table A1 lists references to observations and leaf nitrogen content of natural vegetation. The months and years in which the photosynthesis measurements were made and the location of the study sites (latitudes and longitudes) were specified in the published papers.

Linear mixed-effects model

Our data were not independently sampled. Instead, a hierarchical sampling regime was used to collect the data. Namely, observations were first selected based on location. Within each location, there were samples based on time or species. Observations are likely to be correlated because data from the same location and time could have similar conditions (e.g., soil properties and hydrological conditions) that are not perfectly quantified by the available environmental variables. Thus, simple linear regression assuming independence among observational records was not appropriate for our study. Instead, we applied a linear mixed-effects model (Laird and Ware 1982, Lindstrom and Bates 1988) to account for this correlation among observations, where there were three random effects - the location of the photosynthesis measurement site, plant species and time (months).

The linear mixed-effects model used in this study considered both the area-based leaf nitrogen content and the environmental variables (E) including day length (D), relative humidity (RH), temperature (T) and radiation (R). The form of the model is as follows

$$V_{c,max25} = \alpha + \beta_1 LNC_a + E + \varepsilon_{location} + \varepsilon_{species} + \varepsilon_{time} + \varepsilon, \quad (1)$$

where

$$E = \beta_2 R + \beta_3 D + \beta_4 T + \beta_5 RH, \quad (2)$$

and the error terms are denoted by ε. In Eq.1, the variance of ε is σ^2. The random errors resulting from spatial location, species and time (month) are $\varepsilon_{location}$, $\varepsilon_{species}$, and ε_{month}, respectively. The estimated variance of different error terms are listed in Table A4. We used a similar linear mixed-effects model for J_{max25} (see Table A5 for different error terms).

We used the proportion of variance in observed $V_{c,max25}$ and J_{max25} explained by a certain model (i.e., r^2) to test the strength of the model. To ascertain how much all of the environmental variables contributed to variations in observed $V_{c,max25}$, we first determined the proportion of variation in $V_{c,max25}$ explained by the full model (using all of the environmental variables and leaf nitrogen content as the explanatory variables), which is denoted as r_0^2. Then we obtained the proportion of variation in $V_{c,max25}$ explained by using only leaf nitrogen content as the explanatory variable, which is denoted as r_1^2. The difference between r_0^2 and r_1^2 was the proportion of variation in $V_{c,max25}$ explained by all of the environmental variables (Xu and Gertner 2008). Similarly, the proportion of variation in $V_{c,max25}$ uniquely explained by a single variable (e.g. leaf nitrogen content or temperature) is calculated by the difference in r^2 between the full model and the submodel that includes all variables except for the variable of interest. For example, the proportion of variation in $V_{c,max25}$ contributed by leaf nitrogen content is calculated by subtracting the r^2 of the submodel that includes all the environmental factors from the r^2 of the full model. In a similar fashion, we calculated the impact of environmental variables and leaf nitrogen content on J_{max25}.

Plant functional types (PFTs) & biome regions

Many ESMs simplify the representation of vegetation by dividing species into several simple PFTs (White et al. 2000, Bonan et al. 2003, Sitch et al. 2003, Oleson et al. 2013), due to the computational limitations and our limited understanding of physiological properties of a comprehensive list of species. In these models, each PFT has a particular set of traits and makes up a particular proportion of vegetation at a site. Reich et al. (1997) and Wright et al. (2004) suggested possibilities for building new vegetation schemes that are conceptually cleaner, computationally easier, and that consider trait variation. In this study, we used a common set of plant traits (e.g. growth form, leaf form, and leaf status) and site properties (e.g., region and soil type) (Reich et al. 2007, Kattge et al. 2009, Van Bodegom et al. 2012, van Ommen Kloeke et al. 2012) to our linear mixed-effects model. We grouped species in different combination of PFTs by growth form (herbaceous, shrubs and trees), leaf form (needleleaf and broadleaf), leaf status (evergreen and deciduous), region (tropical, temperate, boreal and artic)and soil type (oxisol or non-oxisol) as an index of soil fertility (Kattge et al. 2009). We stratified the terrestrial vegetation with four levels of PFT definition with increasing complexity. The first PFT definition (PFTD1) consisted of three growth forms only with a total of 3 PFTs. The second PFT definition (PFTD2) included three growth forms, two leaf forms and two leaf status with a total of 9 PFTs. Based on simple combination, PFTD2 would have contained a maximum of 12 PFTs. Our data has 9 PFTs for PFTD2 instead of 12 because other combinations of PFTs do not exist in our data, and the same reasoning hold for the other PFT definitions. The third PFT definition (PFTD3) was comprised of three growth forms, two leaf forms, two leaf status and four regions with a total of 19 PFTs. The last level of PFT (PFTD4) was comprised of three growth forms, two leaf forms, two leaf status, four regions and two soil types with a total of 21 PFTs.

To explore the global pattern of $V_{c,max25}$ and J_{max25}, we divided the globe into different regions, following Spurr & Barnes (1980). Tropical was between 23.5S and 23.5N. The temperate region was between 23.5N and 50N and between 23.5S and 50S. The boreal region was between 50N and 66.5N while the Arctic was from 66.5N to the North Pole.

Results

Global variability of photosynthetic capacity

Our results showed that, at the global scale, species from tropical zones tend to have low $V_{c,max25}$ and J_{max25} while species from higher latitudes tend to have high $V_{c,max25}$ and J_{max25} for all the four different temperature response functions we used (Fig. 2 a,d; and Fig. A1 a,d; A2 a,d; A3 a,d). The high photosynthetic capacity generally results from a higher photosynthetic nitrogen use efficiency of $V_{c,max25}$ or a higher photosynthetic nitrogen use efficiency of J_{max25} rather than a higher leaf nitrogen content (Fig. 2 b,c,e,f; and Fig. A1 b,c,e,f; A2 b,c,e,f; A3 b,c,e,f).

Environmental factors versus leaf nitrogen effects on photosynthetic capacity

Environmental variables contributed to about two times larger amount of variation in observed $V_{c,max25}$ than that of the leaf nitrogen content for TRF2 and TRF3 (Fig. 3a). For TRF1 and TRF4, environmental variables contributed to about 2.5 times larger amount of variation in observed $V_{c,max25}$ than that of the leaf nitrogen content (Fig. 3a). Leaf nitrogen content explained ~17% of the variation in $V_{c,max25}$ for TRF1, TRF2, TRF3, TRF4, while environmental variables jointly explained 36-41% of the variation in $V_{c,max25}$ (Fig. 3a). The percentage of variation in $V_{c,max25}$ explained by the environmental variables using temperature functions with acclimation (36-41%) was similar to without acclimation (39-41%) (Fig. 3a). The primary environmental factors for $V_{c,max25}$ were day length, radiation, temperature and relative humidity in order of decreasing importance (Fig. 4a; and Fig. A5a; A7a; A9a; A11a). Based on our linear mixed-effects model, day length, radiation, relative humidity and leaf nitrogen had positive effects on $V_{c,max25}$, while temperature had negative effects on $V_{c,max25}$ (Fig. 4 b-f; and Fig. A4 b-f; Fig. A6 b-f; Fig. A8 b-f).

Environmental variables contributed to about 6 times larger amount of variation in observed J_{max25} than that of the leaf nitrogen content for TRF3 and TRF4 (Fig. 3a). For TRF1 and TRF2, environmental variables contributed to about 9 times larger amount of variation in observed J_{max25} than that of the leaf nitrogen content (Fig. 3a). Leaf nitrogen content explained ~6% of the variation in J_{max25} for temperature response functions without acclimation (TRF1 and TRF2), while it explained ~9% of the variation in J_{max25} for temperature response functions with acclimation (TRF3 and TRF4). Environmental variables jointly explained ~61% of the variation in J_{max25} when TRF2 and TRF4 were used (Fig. 3b). The percentage of variation in J_{max25} explained by the environmental variables was relatively low for TRF1 and TRF3 (~55%) (Fig. 3b). The key environmental factors for J_{max25} were day length, temperature, radiation, and relative humidity in order of decreasing importance (Fig. 5a; and Fig. A5a; A7a; A9a). Based on our linear mixed-effects model, day length, radiation, relative humidity and leaf nitrogen had positive effects on J_{max25}, while temperature had negative effects on J_{max25} (Fig. 5 b-f; and Fig. A5 b-f; Fig. A7 b-f; Fig. A9 b-f).

In terms of the relative importance of the two pathways through which environmental factors can affect $V_{c,max25}$, our results showed that environmental variables jointly contributed to a small amount of variation in observed leaf nitrogen content for different temperature response functions (4.5-5%; Fig. 6a) compared to their contribution to photosynthetic nitrogen use efficiency of $V_{c,max25}$ (42-49%; Fig. 6a). The largest amount of variation in photosynthetic nitrogen use efficiency of $V_{c,max25}$ ($NUE_{c,max25}$) was explained by day length (33-39%; Fig. 7a; and Fig. A10a - A12a). Radiation, relative humidity and temperature had smaller impact on $NUE_{c,max25}$ (0.6-10%; Fig. 7a; and Fig. A10a - A12a). Together, environmental variables had much more control over photosynthetic nitrogen use efficiency of $V_{c,max25}$ than leaf nitrogen content (Fig. 6a).

In the case of J_{max25}, environmental variables in combination contributed to a small amount of variation in observed leaf nitrogen content for different temperature response functions (~9%) compared to their contribution to photosynthetic nitrogen use efficiency of J_{max25} (52-56%; Fig. 6b). The largest amount of variation in photosynthetic nitrogen use efficiency of J_{max25} ($NUE_{j,max25}$) was explained by day length (31-37%; Fig. 7b; and Fig. A10b - A12b). Radiation, relative humidity and temperature had smaller impact on $NUE_{j,max25}$ (0-17%; Fig. 7b; and Fig. A10b - A12b). Together, environmental variables had much more control over photosynthetic nitrogen use efficiency of J_{max25} than leaf nitrogen content (Fig. 6b). We want to point out that the difference in the explained amount of the variation for leaf nitrogen content is slightly different because different data sets are used for $V_{c,max25}$ and J_{max25} as not all the studies reported both $V_{c,max25}$ and J_{max25}.

Photosynthetic capacity for plant functional types (PFTs)

Our results showed that, across all of the temperature response functions, the model that uses the most comprehensive classification of PFTs (PFT definition 4 with 21 PFTs in Table 3; r^2=40-47%) explained less of the variation in observed $V_{c,max25}$ than the model that only uses leaf nitrogen content and environmental variables (Fig. 8a; r^2=54-58%). For TRF1, TRF2, TRF3 and TRF4, and depending on the PFT grouping methodology, PFT explains 10-47% of the variation in photosynthetic capacity of $V_{c,max25}$ (Fig. 9; and Fig. A13; A15; A17). The addition of environmental variables increased the explanation of variation to 40-54% (Fig. 9; and Fig. A13; A15; A17). Finally, the addition of leaf nitrogen content resulted in a total of 55-64% of variation explained (Fig. 9; and Fig. A13; A15; A17). This indicates that the addition of both environmental variables and leaf nitrogen content to PFTs substantially improves the predictive power of the empirical model of $V_{c,max25}$. Since the PFT definitions 3 and 4 considered growth regions, both definitions implicitly contain the climate information, explaining why including environmental factors with these PFT definitions does not greatly improve the proportion of variation explained (Fig. 9; and Fig. A13; A15; A17). We want to highlight that for every temperature response function (TRF1, TRF2, TRF3 and TFR4), the explained variance of $V_{c,max25}$ by the most comprehensive classification of PFTs (PFT definition 4 with 21 PFTs in Fig. 9; Fig. A13; A15; A17; r^2=40-46%) and by the most comprehensive classification of PFTs combined with environmental variables (Fig. 9; Fig. A13; A15; A17; r^2=49-54%) is lower than the model that only uses leaf nitrogen content and environmental variables (Fig. 9; Fig. A13; A15; A17; r^2=54-58%). This suggests that we will be able to use environmental variables and leaf nitrogen content to make reasonable predictions about the photosynthetic capacity of $V_{c,max25}$ at the global scale, without distinguishing individual PFTs.

Our results also showed that, across all of the temperature response functions, the model that uses the most comprehensive classification of PFTs (PFT definition 4 with 21 PFTs in Fig. 8b; r^2=59-69%) explained less amount of variation in observed J_{max25} than the model that only uses leaf nitrogen content and environmental variables (Fig. 8b; r^2=63-69%). For TRF1, TRF2, TRF3, and TRF4, and depending on the PFT grouping methodology, PFT explains 33-69% of the variation in photosynthetic capacity of J_{max25} (Fig. 10; Fig. A14; A16; A18). The addition of environmental variables increased the explanation of variation to 56-72% (Fig. 10; Fig. A14; A16; A18). Finally, the addition of leaf nitrogen content resulted in a total of 66-76% of variation explained (Fig. 10; Fig. A14; A16; A18). This indicates that the addition of both environmental variables and leaf nitrogen content to PFTs substantially improves the predictive power of the empirical model of J_{max25}. Since the PFT definitions 3 and 4 considered growth regions, both definitions implicitly contain the climate information, explaining why including environmental factors with these PFT definitions does not greatly improve the proportion of variation explained (Fig. 10; Fig. A14; A16; A18). For each temperature response functions, the explained variance of J_{max25} by the most comprehensive classification of PFTs (PFT definition 4 with 21 PFTs in Fig. 10; Fig. A14; A16; A18; r^2=59-69%) and by the most comprehensive classification of PFTs combined with environmental variables (Fig. 10; Fig. A14; A16; A18; r^2=64-68%) is similar to the model that only uses leaf nitrogen content and environmental variables (Fig. 10; Fig. A14; A16; S18; r^2=63-69%). This suggests that we will also be able to use environmental variables and leaf nitrogen content to make reasonable predictions about the photosynthetic capacity of J_{max25} at the global scale, without distinguishing individual PFTs.

Discussion

Variation in photosynthetic capacity with latitude

Our results showed that species from tropical zones tend to have relatively low $V_{c,max}$ and J_{max25} values. This finding is consistent with Kattge et al. (2009). There are three important hypotheses about photosynthetic capacity that could explain why $V_{c,max}$ and J_{max25} increase with latitude. Firstly, plants from high latitudes need to invest more nitrogen in Rubisco to offset the marked reduction in carboxylation at low temperatures. Without increased investment in Rubisco, these plants could not sustain a positive carbon balance at low temperature (Kerkhoff et al. 2005). This hypothesis is supported by our data showing that a higher $NUE_{c,max25}$ is associated with plants from high latitudes. Secondly, plants from lower latitudes may need to retain leaves for a longer period in order to both endure shade (Reich et al. 2004) and to invest more nitrogen in traits associated with leaf toughness, longevity and resistance to pests and pathogens, rather than to tissues leading to high productivity (Kikuzawa et al. 2013). Therefore, for a given nitrogen content, plants from lower latitudes may have a lower photosynthetic capacity (Reich et al. 1991b, Prior et al. 2003, Hikosaka 2005). Finally, the growing season day length could be another important factor contributing to the latitudinal pattern, in view that longer day length at high latitudes could lead to higher $V_{c,max25}$ and higher J_{max25}. Longer day length could be associated with longer photoperiod, which has been demonstrated by previous studies to alter $V_{c,max25}$ and J_{max25} (Comstock and Ehleringer 1986, Bauerle et al. 2012). The mechanism of this acclimation could be related to photoperiod sensing and regulations, which may modify the gene expressions in plants (e.g.Song et al. 2013). Previous studies has shown that photosynthetic capacity of Pinus banksiana seedlings was reduced by instituting a short-day treatment in the fall, but maintaining high summer growth temperatures (Busch et al. 2007, 2008).

Causes of variability in photosynthetic capacity

In our global scale study, we found that environmental factors affected the photosynthetic capacity mainly through the impact on photosynthetic nitrogen use efficiency, rather than through leaf nitrogen content. This result is in agreement with previous studies showing large variation in the relationship between leaf nitrogen content and photosynthesis (Evans 1989). However, it is in disagreement with Niinemets et al. (1998)'s finding that the change in area-based leaf nitrogen content resulting from leaf morphological plasticity (e.g. leaf mass per unit area) contributes much more to the photosynthetic capacity under light gradients than the variations in nitrogen use efficiency resulting from changes in nitrogen investment. This discrepancy could be attributed to the fact that at the global scale, there is a large amount of variation in leaf nitrogen content with a large number of species (>100 species in this study compared to 4 species in Niinemets et al. (1998)'s study) and thus the impact of leaf nitrogen content on $V_{c,max25}$ became weaker, especially compared to variation within a single species where changes in leaf mass per area explain the vast majority of vertical variation in leaf nitrogen (e.g. Ellsworth and Reich 1993). This argument is supported by Feng & Dietze (2013)'s recent finding that relationships between leaf traits and photosynthesis established at broad scales, such as across biome relationships, may not be captured at finer scales. Furthermore, if we only consider the radiation impact on $V_{c,max25}$, our results suggest that radiation explained little amount of the variation in leaf nitrogen and in $NUE_{c,max25}$ (~2%; Fig. 7a). We want to point out that variations in nitrogen use efficiency can be caused by several different factors including leaf age (Escudero and Mediavilla 2003), nitrogen allocation to photosynthetic apparatus (Xu et al. 2012), and specific activity and activation states of photosynthetic enzymes (Poorter and Evans 1998). Currently, we do not have data on the above factors to point out the specific mechanistic process contributing to the variation in nitrogen use efficiency.

Hypotheses on environmental control of $V_{c,max25}$

Our result supports some of the hypotheses on environmental control of $V_{c,max25}$ at the global scale. Firstly, our study supports the hypothesis that $V_{c,max25}$ is higher at a lower growth temperature. This could be attributed to temperature acclimation due to changes in photosynthetic enzyme properties (Bunce 1998, Hikosaka et al. 2005) or in the nitrogen investment (Onoda et al. 2005, Yamori et al. 2005). Using a nitrogen allocation model based on a trade-off of nitrogen allocated between growth and storage, and an optimization of nitrogen allocated among light capture, electron transport, carboxylation, and respiration to maximize photosynthesis, Xu et al. (2012) predicted that plants tend to invest higher amount nitrogen for $V_{c,max25}$ and lower amount of nitrogen for J_{max25} and storage. Secondly, our study supports the hypothesis that $V_{c,max25}$ is higher at a higher irradiance, which is in agreement with the results from Maire et al. (2012). This finding is also in agreement with the optimization hypothesis proposed by Haxeltine & Prentice (1996) and Dewar (1996), who suggested that in theory, plants may have a high photosynthetic capacity due to increased leaf nitrogen content under elevated radiation levels. Haxeltine & Prentice (1996) developed a general model based on Farquhar's model of photosynthesis for light-use efficiency of primary production, which linked photosynthetic capacity and area-based leaf nitrogen content. Their approach was based on the optimization theory that maximized net assimilation (photosynthesis minus leaf respiration) against incoming radiation. Dewar (1996) did similar work to Haxeltine & Prentice (1996), except that he maximized net photosynthesis at each canopy level. The results of Haxeltine & Prentice (1996) and Dewar (1996) imply that once the photosynthetic properties of leaves have adjusted to a given (and constant) daily pattern of radiation, then their daily light use efficiency is constant.

Uncertainties in data analysis and mechanistic interpretation

One potential uncertainty can result from the temperature responses that we used to scale $V_{c,max}$ and J_{max} to $V_{c,max25}$, J_{max25}, respectively. We used four versions of temperature dependence functions of $V_{c,max}$ (see methodology) to assess the effects of potential bias in temperature response estimation on our analyses. Specifically, we used temperature response functions from (1) Collatz et al. (1991) and Sellers et al. (1996) which was based on the Q_{10} concept (2) a temperature response function proposed by Leuning (2002) (3) a temperature response function based on Kattge & Knorr (2007)'s formulation of acclimation, where temperature optimum was a function of growth temperature, and (4) a temperature response function based on Kattge & Knorr (2007)'s formulation but with limited temperature acclimation, where the plant's growth temperature was constrained between 11°C and 35°C. The main difference among these four functions is that the temperature response diverges at temperatures more than 30°C (Fig. 1).

Environmental variables contributed to a relatively lower amount of variation in observed $V_{c,max25}$ and J_{max25} for TRF3 than for TRF1, TRF2, and TRF4. When Kattge & Knorr (2007)'s formulation of temperature acclimation was used (TRF3 and TRF4), a lower $V_{c,max25}$ and J_{max25} was generally associated with plant growth temperatures less than 15°C and more than 25°C relative to without the acclimation case (TRF2) (Fig. A19a). The temperature acclimations did not substantially change the standardized values of $V_{c,max25}$ or J_{max25} at relative high growth temperatures because most of the relatively high measurement temperatures were around 25°C (Fig. A19b). Meanwhile, the temperature acclimations can lead to lower values of $V_{c,max25}$ or J_{max25} at the lower measurement temperatures. Therefore, the temperature acclimations can lead to a smaller variations in $V_{c,max25}$ and J_{max25} across the environmental gradient (e.g. day length, Fig. A19c; A19d). As a result, temperature response functions that assumed unlimited temperature acclimation (TRF3) fitted the data a little poorer than temperature response functions that did not assume acclimation (TRF1 and TRF2). The temperature responses function with limited acclimation (TRF4) fit the data almost as good as TRF1 and TRF2 because it limited temperature acclimation to the range between 11°C and 35°C. Overall, our result of the relative impact of environmental factors and leaf nitrogen on photosynthetic capacity holds for different types of temperature response functions.

While we have analyzed the most comprehensive data set currently available, we are aware that the data set needs improvement. For example, the data set lacks information on various mechanistic processes, which might explain the relationships we observed in the data set. Our proposed method is purely correlational. It does not explain mechanistically the acclimation, phenotypic plasticity, and turnover processes behind the statistical relationships between $V_{c,max25}$ or J_{max25} and environmental variables nor does it account for trait trade-offs. Still, in our opinion, it is an important and necessary step as it reflects the observed correlations between traits and climate drivers (Wright et al. 2005, Martin-StPaul et al. 2012). Importantly, we quantified the key environmental predictors for $V_{c,max25}$ or J_{max25} using a linear mixed model that captures a large part of observed trait variation despite large variations among species. Furthermore, our study shows that leaf nitrogen and environmental conditions alone are as good predictors of photosynthetic capacity as functional type classifications or even functional type classification combined with leaf nitrogen. This is an important step for future progress towards developing models that can be used to more reliably predict future photosynthetic capacities.

Implications for dynamic global vegetation modeling

It has been suggested that we should improve the representation of $V_{c,max}$ and J_{max} in ESMs by using more or different groupings of PFTs; however, simply increasing the number of PFTs is challenging both for computational reasons and because our understanding of the mechanisms governing the distribution of even the most broad definitions of PFTs is poor. Our findings about the environmental control on photosynthetic capacity are consistent with the finding from Verheijen et al. (2012). Verheijen et al. (2012) illustrated that allowing traits within PFTs to vary with plant trait – climate relationships yielded a closer match to some types of observational data. The results of our study could be incorporated into a similar modeling framework to improve prediction of future global carbon dynamics.

One important result from our study is that when we included the leaf nitrogen content and environmental variables, depending on the temperature response function used, all four groupings of PFTs explained a similar amount of variation in $V_{c,max25}$ (Fig. 9; Fig. A13; A15; A17). The same was true for J_{max25} (Fig. 10; A14; A16; A18). These suggest that, with the inclusion of environmental variables and leaf nitrogen content, we should be able to successfully predict the photosynthetic capacity with relatively few PFTs. Our findings demonstrate functional convergence, that is, even across contrasting PFTs, at the scale of leaf, fundamental physiological constraints apply (Schulze et al. 1994, Reich et al. 1997, Meinzer 2003). Reich et al. (1997) demonstrated the concept of functional convergence, whereby, universal constraints, or trade-offs, among fundamental leaf traits such as nitrogen content, life-span, photosynthetic capacity and leaf mass per area were found to apply across hundreds of species native to a wide range of biomes from the tropics to tundra. Our findings provide a clear physiological reason why we can simplify some of our models and therefore have important implications for interpreting and modeling vegetation properties such as productivity across a broad range of scales.

Another important result is that, the inclusion of leaf nitrogen content and environmental variables to any one of the four groupings of PFTs explained a similar amount of variation in $V_{c,max25}$ (depending on the temperature response function used) as the model that considered environmental variables and leaf nitrogen content without PFTs (Fig. 9; Fig. A13; A15; A17). The same was true for J_{max25} (Fig. 10; A14; A16; A18). These suggest that environmental variables and leaf nitrogen content can predict most of the variation in the photosynthetic capacity, and therefore we do not need to consider PFTs for $V_{c,max25}$ and J_{max25} estimation.

The environmental control of $V_{c,max25}$ and J_{max25} could have important implications for predicting vegetation dynamics and carbon fluxes. Some ESMs have already incorporated the effect of seasonal variation in relative day length at the pixel level on $V_{c,max25}$ and J_{max25}

(Bauerle et al. 2012); however, as far as we know, most ESMs have not incorporated effects of temperature, radiation, day length and humidity on $V_{c,max25}$ and J_{max25} at the global scale. For the high latitudes (boreal and arctic), where the most dramatic warming is predicted to occur (Bonan 2008, Bader 2014, Ding et al. 2014), the temperature effects on $V_{c,max25}$ (Xiang et al. 2013) could be important to predict vegetation responses to warming. Our analysis suggests that as high latitudes warm, $V_{c,max25}$ should decrease. Therefore, not accounting for the correlation between temperature and $V_{c,max25}$ would lead to an overestimation of photosynthetic capacity and thus an overestimation of gross primary production in future warmer high latitude ecosystems. With a $V_{c,max25}$ of 91.6 µmol CO_2 m^{-2} s^{-1} and a J_{max25} of 205.7 µmol electron m^{-2} s^{-1} based on our arctic data, acclimation in $V_{c,max25}$ and J_{max25} due to a 5°C increase in temperature would reduce photosynthesis by 36% (see Appendix C) relative to what would occur in the absence of down-regulation. Regardless of whether plants acclimate to temperature or not, warming increased photosynthesis. The increment of photosynthesis was lower when acclimation was assumed than without acclimation. We want to point out that CO_2 is a key environmental factor that could affect $V_{c,max25}$ and J_{max25} (Medlyn et al. 1999, Ainsworth and Rogers 2007). In this study, we do not examine the importance of atmospheric CO_2 concentration due to the potential bias as a result of a limited number species under elevated CO_2. Future studies that link the atmospheric CO_2 concentration with temperature, radiation and humidity to assess their impact on $V_{c,max25}$ and J_{max25} could be critical for our prediction of photosynthesis rates under climatic change.

Future work & caveats

The results of our study suggest that at the global scale, environmental variables have much stronger control on plant photosynthetic capacity than the area-based leaf nitrogen content.

Our normalized dataset could be used as a basis for development and parameterization of more mechanistic models (e.g. Xu et al. 2012). Such models can be very useful for understanding carbon-nitrogen coupling at the leaf scale and simulating the acclimation of photosynthetic capacity to temperature in ESMs. However, there are still caveats that should be considered. First, although environmental and leaf nitrogen content values explained a large part of variability in photosynthetic capacity, there is still significant uncertainty that cannot be explained – which could be attributed to other constraints such as leaf life span (Wright et al. 2004, Reich et al. 2007), phosphorus limitation (Lewis et al. 1994, Warren 2011), leaf thickness (Wright and Westoby 2002), leaf development (Wilson et al. 2000, Xu and Baldocchi 2003, Grassi et al. 2005), leaf nonstructural carbohydrate content (Misson et al. 2006), soil water content (Nogues and Alegre 2002), soil temperature (Misson et al. 2006), and pH of the soil or rooting depth (Canadell et al. 1996). To our knowledge, only a few studies have looked at the effects of the above factors on photosynthetic capacity and therefore, at this time, it is not possible to examine how these factors would control the plant photosynthetic capacity at the global scale.

Second, in this study, we used mean monthly environmental variables. Thus, our results are focused on an intermediate time scale. A different interpretation of the impacts of these environmental variables on photosynthetic capacity could result from considering short-term (daily basis) or long-term (yearly or decadal) scales. In the short-term (daily basis), variation in environmental variables may explain only a small amount of the variation in photosynthetic capacity (Xu and Baldocchi 2003). In the long-term, environmental variables could cause up to two fold inter-annual variations in photosynthetic capacity (Grassi et al. 2005, Kitaoka and Koike 2005, Iio et al. 2008). Because the response of photosynthesis to these environmental drivers is nonlinear, the response derived from monthly mean environmental conditions could be very different form the mean of the daily responses. For example, strong seasonal and diurnal variability in the magnitudes of temperature increase may shift the photosynthesis-temperature relationships of plants by altering the balance between $V_{c,max}$ and J_{max} and changing temperature optima (Billings et al. 1971, Berry and Björkman 1980, Wilson et al. 2000, Onoda et al. 2004, 2005).

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Conflict of Interest

None declared.

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Supporting Information Additional Supporting Information may be found in the online version of this article:

Appendix A Shows a list of published literature sources and further details of linear mixed effects analyses using various temperature response functions mentioned in the text.

Appendix B Relationship between photosynthetic capacity and other variables, including statistic.

Appendix C Effect of temperature acclimation on leaf photosynthesis (*A*).

Appendix D Temperature dependence of kinetic properties of Rubisco**.**

Appendix E Temperature dependence of $V_{c,max}$ and J_{max}**.**

Appendix F The Farquhar Photosynthesis & Ball-Berry model.

Appendix G Standardization of $V_{c,max25}$ and J_{max25}.

Supplementary Photosynthetic and climate data associated with this paper. The dataA.txt file defines various acronyms for temperature response functions. The classifications of various plant functional types are shown in dataB.txt. The climate variables and standardized values of $V_{c,max25}$ and J_{max25} are presented in dataC.txt. dataD.txt contains standardized values of $V_{c,max25}$ and J_{max25} and temperature response functions are identified.

Figure Captions

Figure 1 Temperature (°C) response curves for $V_{c,max}$ (μmol CO_2 m^{-2} s^{-1}) using four different temperature response functions; TRF1 (black dashed), TRF2 (black dotdash), TRF3 at two growth temperatures; 6°C and 30°C ($TRF3_6$; blue longdash, $TRF3_{30}$; blue twodash), and TRF4 at two growth temperatures; 6°C and 30°C ($TRF4_6$; green longdash, $TRF4_{30}$; green twodash). The dashed vertical lines indicate the range of the measured temperature (6°C to 34°C) at which measured $V_{c,max}$ was reported by the studies.

Figure 2 Box plots of individual data points of $V_{c,max25}$, photosynthetic nitrogen use efficiency of $V_{c,max25}$ ($NUE_{c,max25}$), J_{max25}, photosynthetic nitrogen use efficiency of J_{max25} ($NUE_{j,max25}$) and leaf nitrogen content (LNC_a) by latitude (a,b,c,d,e,f). $V_{c,max25}$, $NUE_{c,max25}$, $NUE_{j,max25}$ and LNC_a were binned at latitude in correspondence with their biome regions; Temperate region in the South of Equator (Temp(S)), Tropical, Temperate region in the North of Equator (Temp(N)), Boreal and Arctic. We used TRF4 as the temperature response function. See Appendix Figure A1-3 for other temperature response curves.

Figure 3 Percentage of variation in (a) $V_{c,max25}$ (μmol CO_2 m^{-2} s^{-1}) and (b) J_{max25} (μmol electron m^{-2} s^{-1}) using different temperature response functions (TRFs) explained by the sum of the local environmental variables (E) and leaf nitrogen content (LNC_a; gN m^{-2}). Temperature response function 1 (TRF1) is adapted from Collatz et al. (1991) and Sellers et al. (1996), TRF2 is a temperature response function proposed by Leuning (2002), TRF3 is a temperature response function based on Kattge & Knorr (2007)'s formulation of acclimation, where temperature optimum was a function of growth temperature, and TRF4 is based on Kattge & Knorr (2007)’s formulation but with limited temperature acclimation, where the plant’s growth temperature was constrained between 11°C and 35°C. See Appendix G for details of different temperature response functions.

Figure 4 Percentage of variation in $V_{c,max25}$ (µmol CO$_2$ m^{-2} s^{-1}) explained by area-based leaf nitrogen content (LNC_a; gN m^{-2}) and all of the environmental variables (E) are shown (a), where the specific environmental variables include day length (D; hours), daytime radiation (R; W m^{-2}), growth temperature (T; °C), relative humidity (RH; unitless), and “$\tilde{E}$” includes daytime radiation, growth temperature and relative humidity. The relationship between $V_{c,max25}$ and environmental variables including day length (b), daytime radiation (c), temperature (d), relative humidity (e), and leaf nitrogen content (f) with the grey solid line estimated from linear mixed-effects model. The data points correspond to an individual leaf. The coefficient of the regression and corresponding p-values (in the parentheses) is shown in different panels. We used TRF4 as the temperature response function. See Appendix Figure A4, A6 and A8 for other temperature response curves.

Figure 5 Percentage of variation in J_{max25} (µmol electron m^{-2} s^{-1}) explained by area-based leaf nitrogen content (LNC_a; gN m^{-2}) and all of the environmental variables (E) are shown (a), where the specific environmental variables include day length (D; hours), daytime radiation (R; W m^{-2}), growth temperature (T; °C), relative humidity (RH; unitless), and “$\tilde{E}$” includes daytime radiation, growth temperature and relative humidity. The relationship between J_{max25} and environmental variables including day length (b), daytime radiation (c), temperature (d), relative humidity (e), and leaf nitrogen content (f) with the grey solid line estimated from linear mixed-effects model. The data points correspond to an individual leaf. The coefficient of the regression and corresponding p-values (in the parentheses) is shown in different panels. We used TRF4 as the temperature response function. See Appendix Figure A5, A7 and A9 for other temperature response curves.

Figure 6 Percentage of variations in photosynthetic nitrogen use efficiency of $V_{c,max25}$ ($NUE_{c,max25;}$ μmol CO_2 $g^{-1}N$ s^{-1}) (a), leaf nitrogen content (LNC_a; gN m^{-2}) (a,b) and photosynthetic nitrogen use efficiency of J_{max25} ($NUE_{j,max25;}$ μmol electron $g^{-1}N$ s^{-1}) (b) explained by the sum of the local environmental variables (E) using different temperature response functions (TRF). Original dataset (a) and a subset of the original data that reported J_{max} values was used (b). Thus, data sets for leaf nitrogen contents differed for $V_{c,max25}$ and J_{max25}. The nitrogen use efficiency of $V_{c,max25}$ (a) while Fig. 6b is for the nitrogen use efficiency of J_{max25}. Temperature response function 1 (TRF1) is adapted from Collatz et al. (1991) and Sellers et al. (1996), TRF2 is a temperature response function proposed by Leuning (2002), TRF3 is a temperature response function based on Kattge & Knorr (2007)'s formulation of acclimation, where temperature optimum was a function of growth temperature, and TRF4 is based on Kattge & Knorr (2007)'s formulation but with limited temperature acclimation, where the plant's growth temperature was constrained between 11°C and 35°C. See Appendix G for details of different temperature response functions.

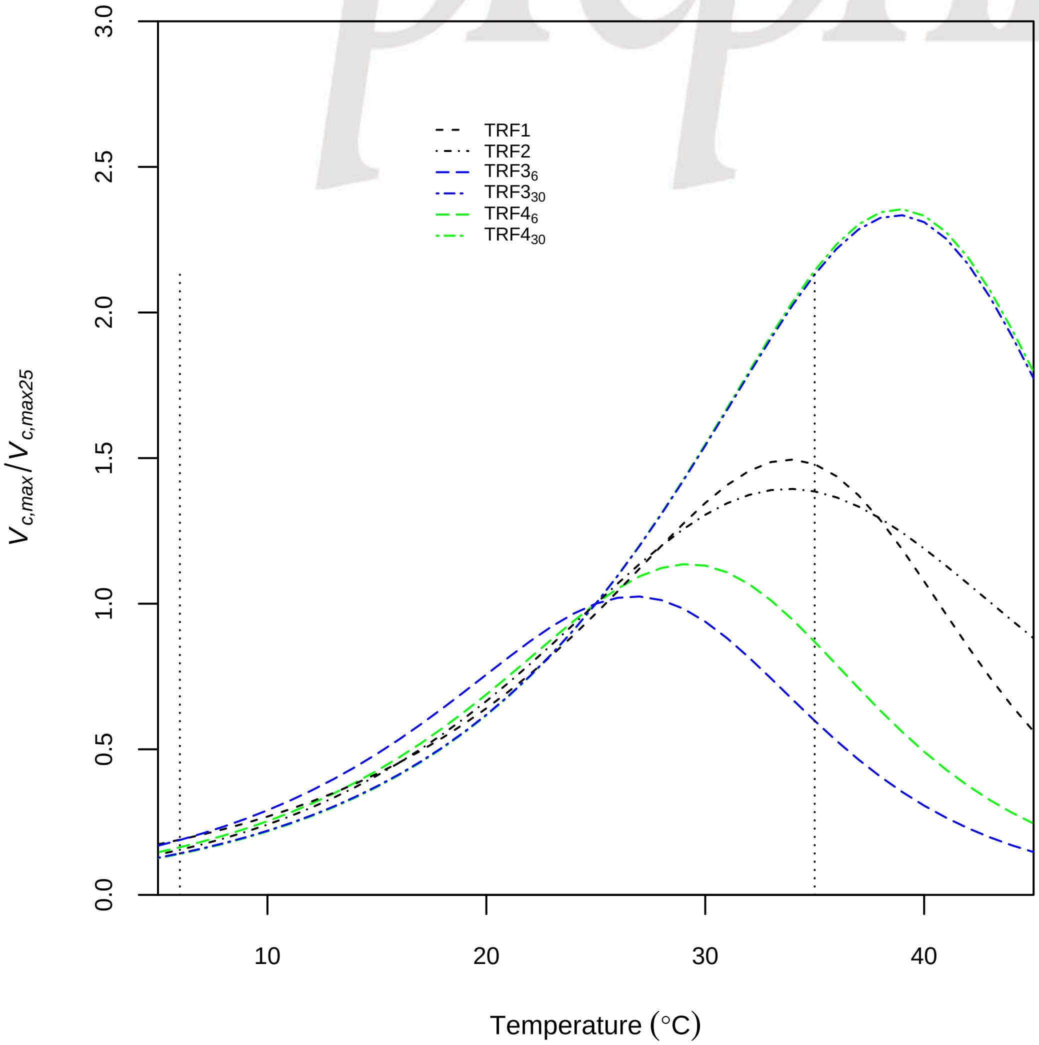
Figure 7 Percentage of variations in (a) photosynthetic nitrogen use efficiency of $V_{c,max25}$ ($NUE_{c,max25;}$ μmol CO_2 $g^{-1}N$ s^{-1}), leaf nitrogen content (LNC_a; gN m^{-2}) and (b) photosynthetic nitrogen use efficiency of J_{max25} ($NUE_{j,max25;}$ μmol electron g^{-1}N s^{-1}) explained by all of the environmental variables (E), where the specific environmental variables include day length (D; hours), daytime radiation (R; W m^{-2}), temperature (T; °C), and relative humidity (RH; unitless). We used TRF4 as the temperature response function. See Appendix Figure A10-12 for other temperature response curves.

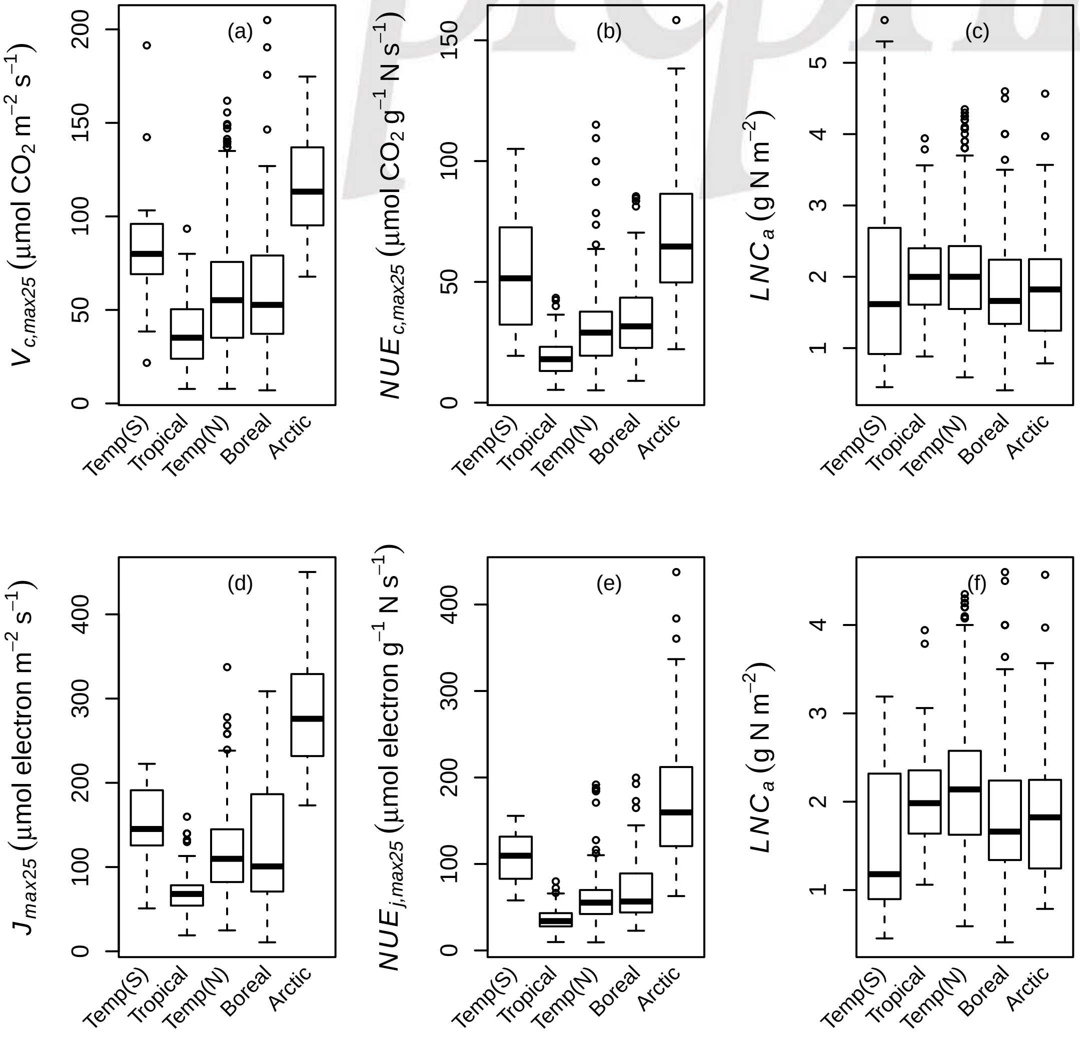
Figure 8 Percentage of variation in (a) $V_{c,max25}$ (μmol CO_2 m^{-2} s^{-1}) and (b) J_{max25} (μmol electron m^{-2} s^{-1}) using different temperature response functions (TRF) explained by the most comprehensive PFT definition 4 (PFTD4) that consisted of growth form, leaf form, leaf status, region and soil type (total of 21 PFTs) and by the sum of the local environmental variables (*E*) and leaf nitrogen content (LNC_a; gN m^{-2}). Temperature response function 1 (TRF1) is adapted from Collatz et al. (1991) and Sellers et al. (1996), TRF2 is a temperature response function proposed by Leuning (2002), TRF3 is a temperature response function based on Kattge & Knorr (2007)'s formulation of acclimation, where temperature optimum was a function of growth temperature, and TRF4 is based on Kattge & Knorr (2007)'s formulation but with limited temperature acclimation, where the plant's growth temperature was constrained between 11°C and 35°C. See Appendix G for details of different temperature response functions.

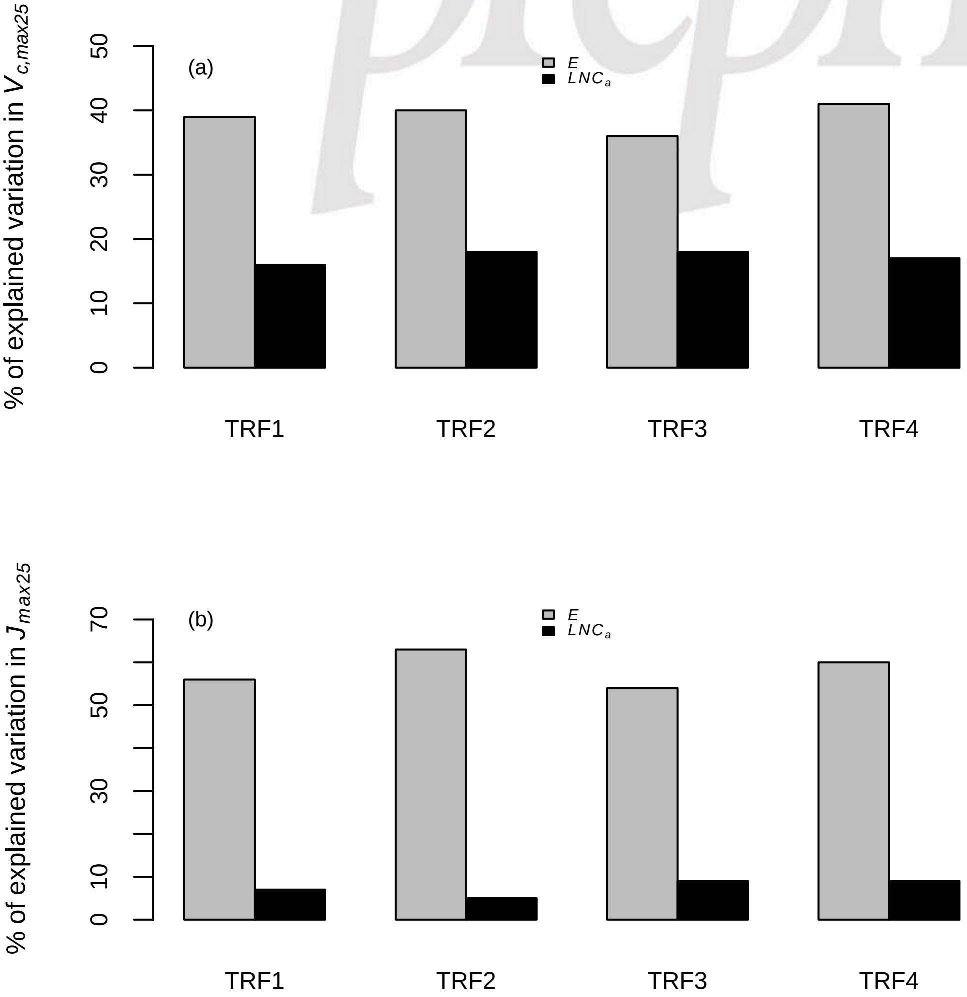
Figure 9 Percentage of variations in $V_{c,max25}$ explained by different plant functional types (PFT), environmental variables (E) and leaf nitrogen content (LNC_a). Species were grouped in 4 different combination of plant functional types (PFTs) by using the growth form (herbaceous, shrubs and trees), leaf form (needleleaf and broadleaf), leaf status (evergreen and deciduous), region (tropical, temperate, boreal and artic) and soil type (oxisol or non-oxisol). PFT definition

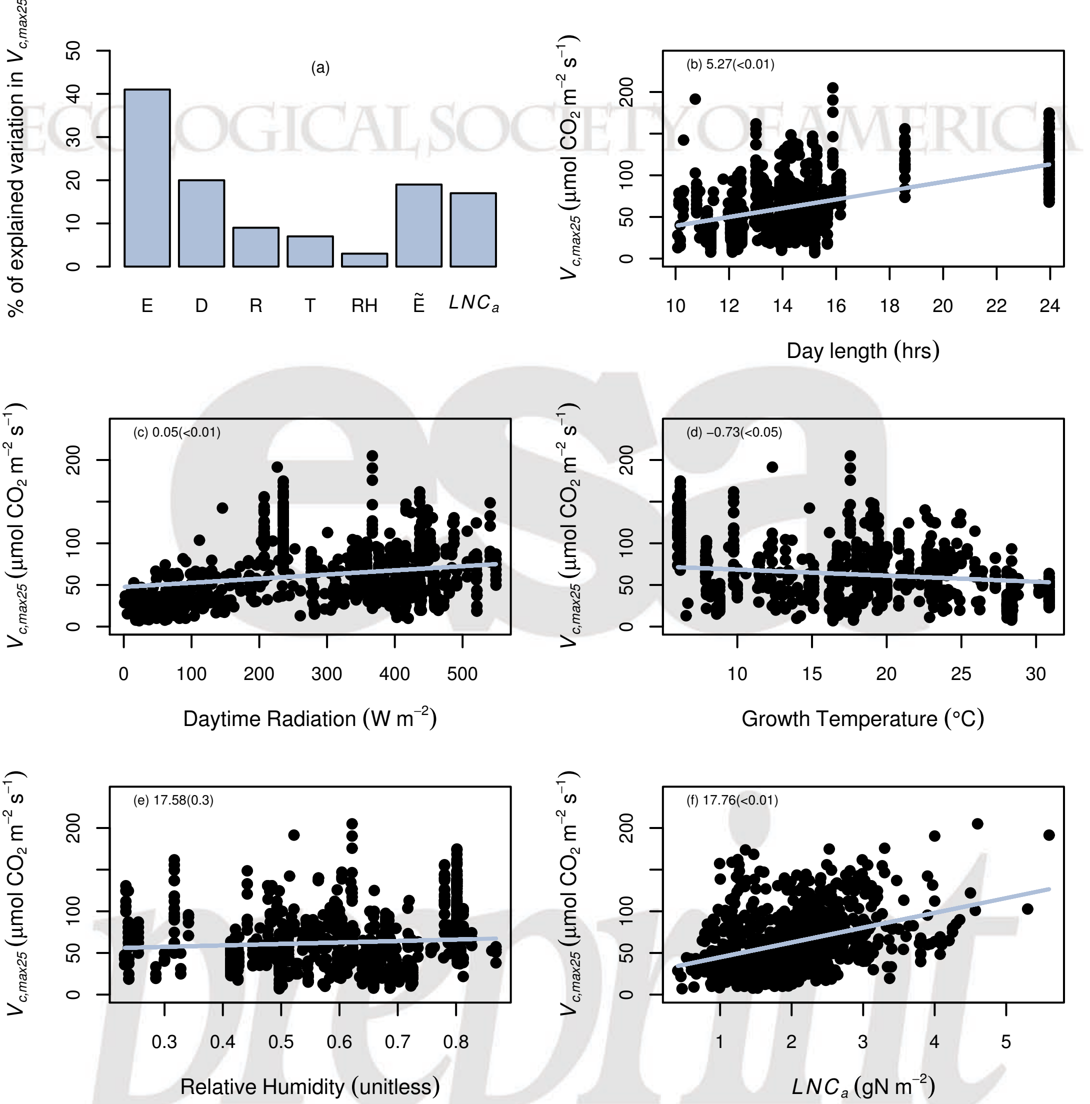
1 (PFTD1) consisted of growth form only (total of 3 PFTs), PFT definition 2 (PFTD2) included growth form, leaf form and leaf status (total of 9 PFTs), PFT definition 3 (PFTD3) comprised of growth form, leaf form, leaf status and region (total of 19 PFTs), and PFT definition 4 (PFTD4) comprised of growth form, leaf form, leaf status, region and soil type (total of 21 PFTs).The dashed line indicates the amount (55%) of the variation in $V_{c,max25}$ explained by environmental variables and LNC_a. We used TRF4 as the temperature response function. See Appendix Figure A13, A15, and A17 for other temperature response curves.

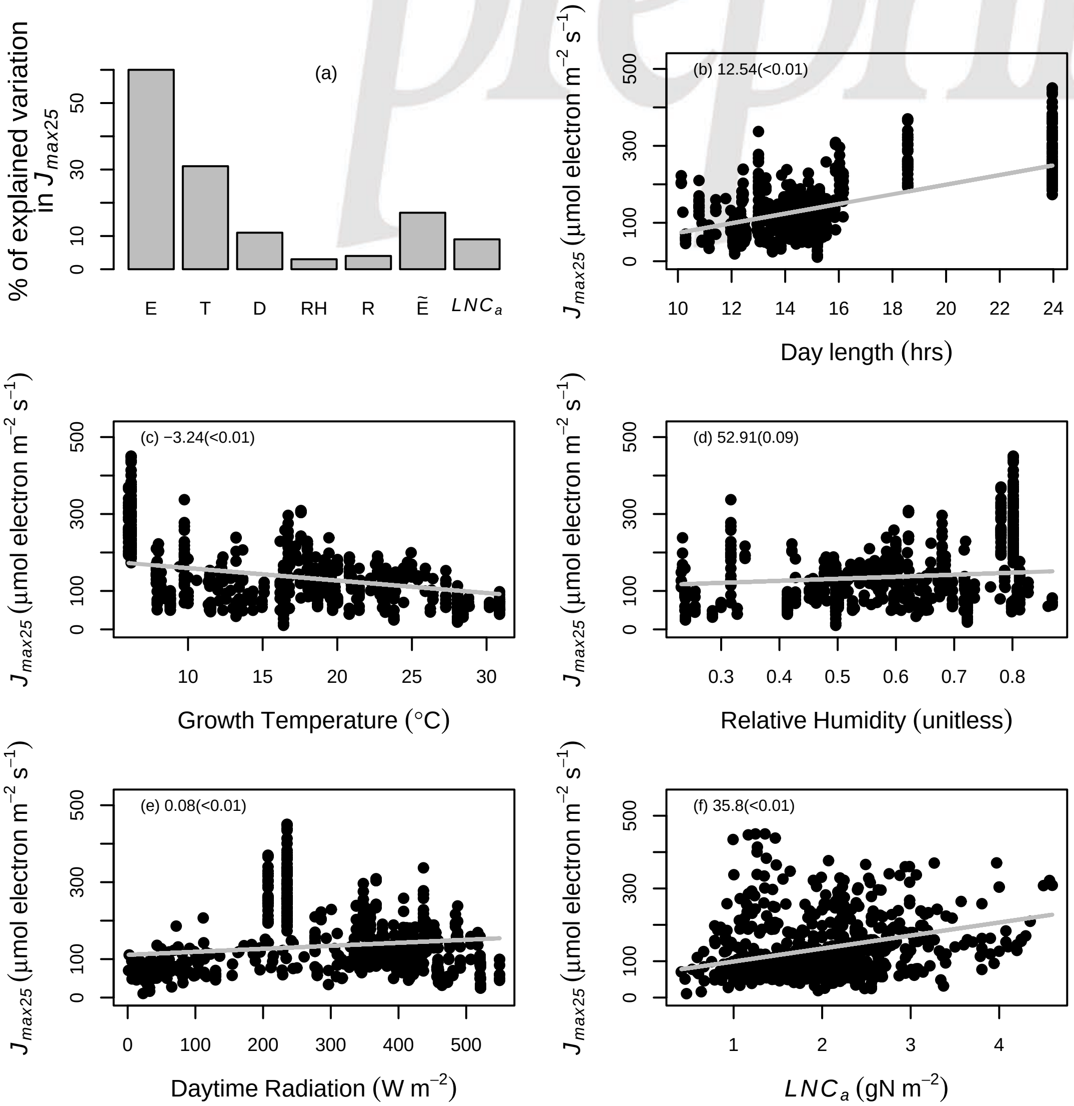
Figure 10 Percentage of variations in J_{max25} explained by different plant functional types (PFT), environmental variables (E) and leaf nitrogen content (LNC_a). Species were grouped in 4 different combination of plant functional types (PFTs) by using the growth form (herbaceous, shrubs and trees), leaf form (needleleaf and broadleaf), leaf status (evergreen and deciduous), region (tropical, temperate, boreal and artic) and soil type (oxisol or non-oxisol). PFT definition 1 (PFTD1) consisted of growth form only (total of 3 PFTs), PFT definition 2 (PFTD2) included growth form, leaf form and leaf status (total of 9 PFTs), PFT definition 3 (PFTD3) comprised of growth form, leaf form, leaf status and region (total of 19 PFTs), and PFT definition 4 (PFTD4) comprised of growth form, leaf form, leaf status, region and soil type (total of 21 PFTs).The dashed line indicates the amount (64%) of the variation in $V_{c,max25}$ explained by environmental variables and LNC_a. We used TRF4 as the temperature response function. See Appendix Figure A14, A16 and A18 for other temperature response curves.

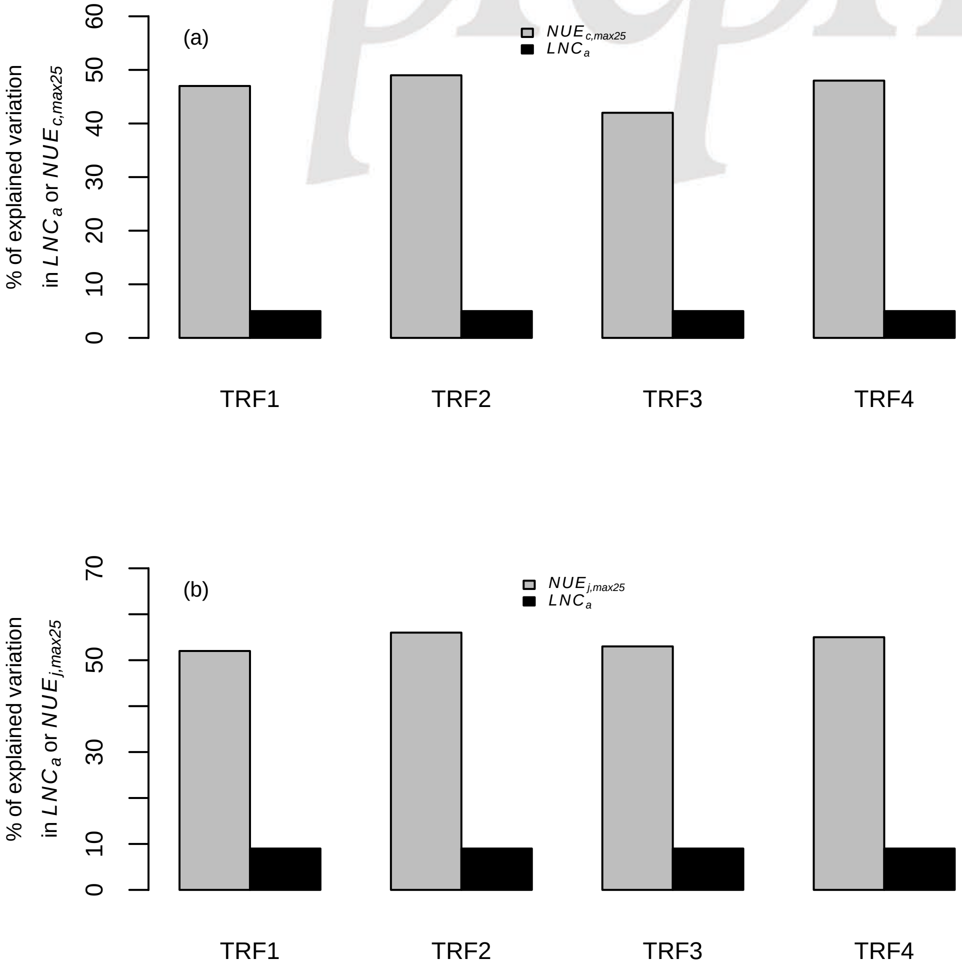

3.0
2.5
2.0
1.5
1.0
0.5
0.0
$V_{c,max}/V_{c,max25}$
TRF1
TRF2
TRF3$_{6}$
TRF3$_{30}$
TRF4$_{6}$
TRF4$_{30}$
10
20
30
40
Temperature (°C)

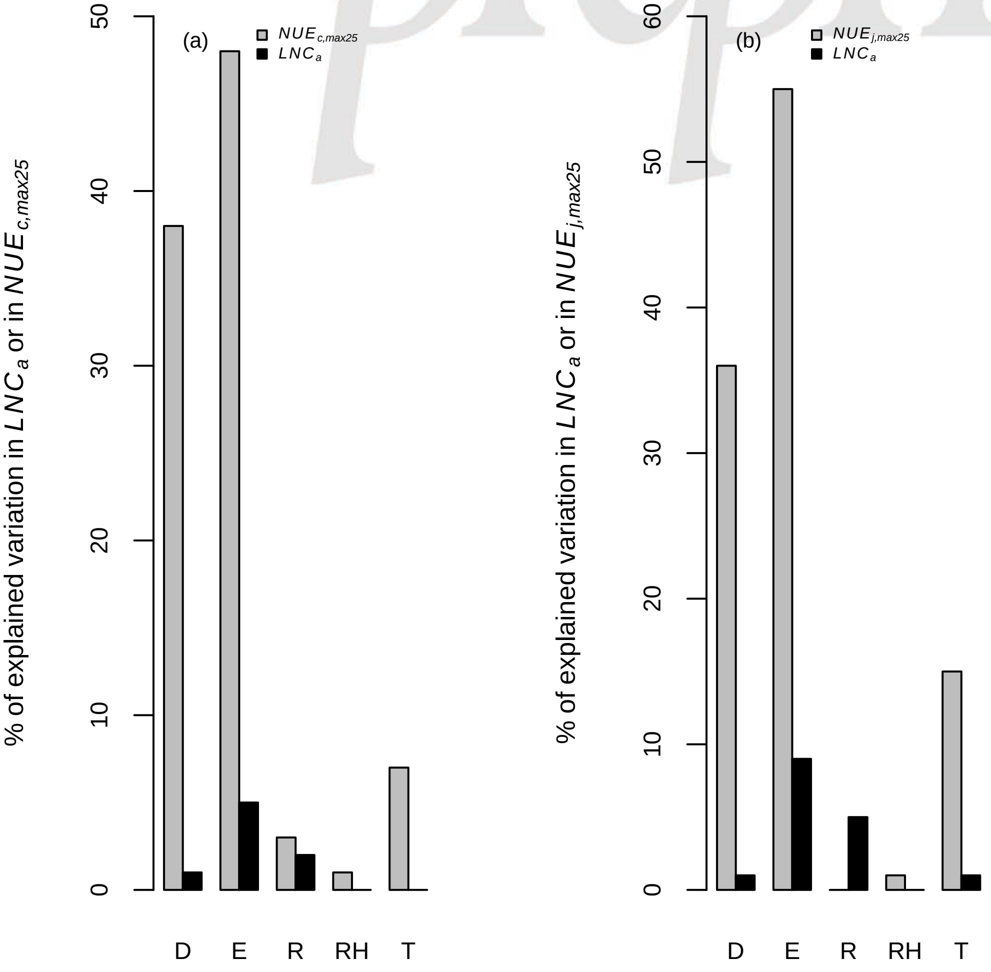

(a)
$V_{c,max25}$ (μmol CO$_2$ m^{-2} s^{-1})
0
50
100
150
200
(b)
$NUE_{c,max25}$ (μmol CO$_2$ g^{-1} N s^{-1})
0
50
100
150
(c)
LNC_a (g N m^{-2})
1
2
3
4
5
(d)
J_{max25} (μmol electron m^{-2} s^{-1})
0
100
200
300
400
(e)
$NUE_{j,max25}$ (μmol electron g^{-1} N s^{-1})
0
100
200
300
400
(f)
LNC_a (g N m^{-2})
1
2
3
4
Temp(S)
Tropical
Temp(N)
Boreal
Arctic

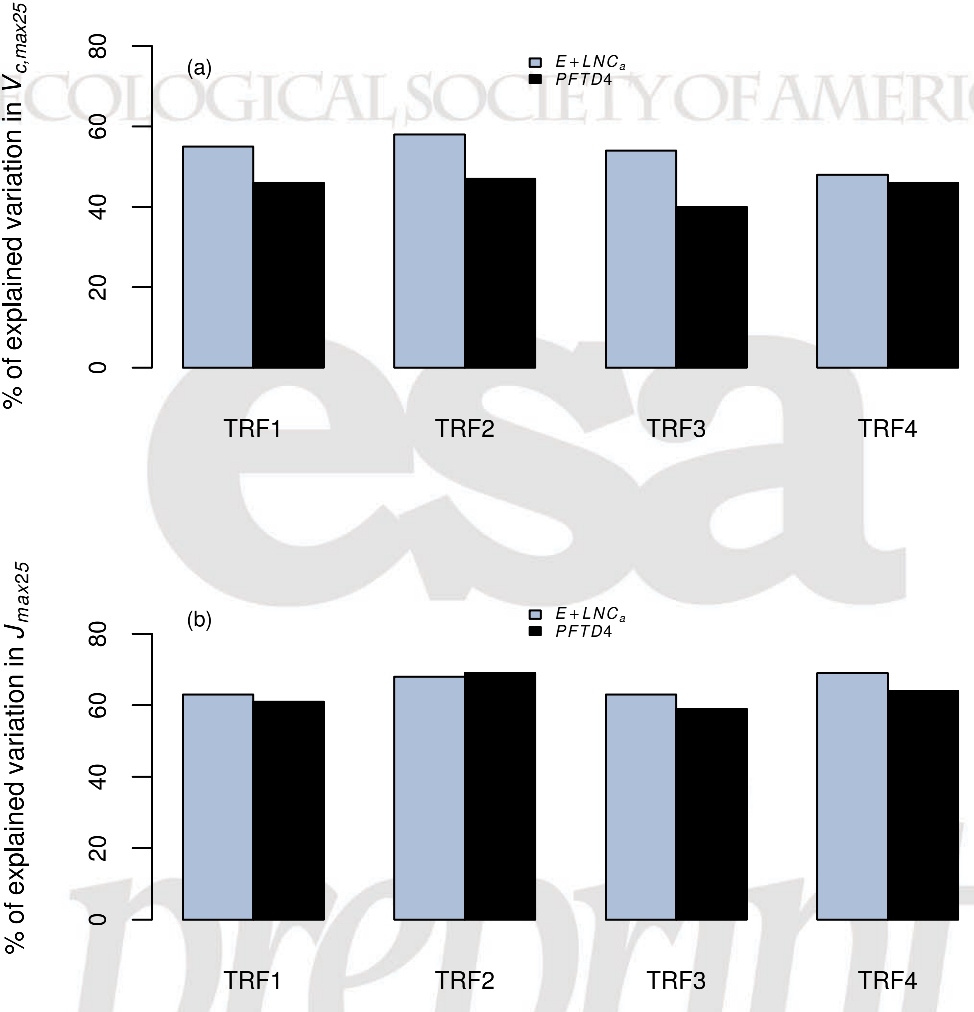

(a)
% of explained variation in $V_{c,max25}$
0
10
20
30
40
50
▨ E
■ LNC_a
TRF1
TRF2
TRF3
TRF4
(b)
% of explained variation in J_{max25}
0
10
30
50
70
▨ E
■ LNC_a
TRF1
TRF2
TRF3
TRF4

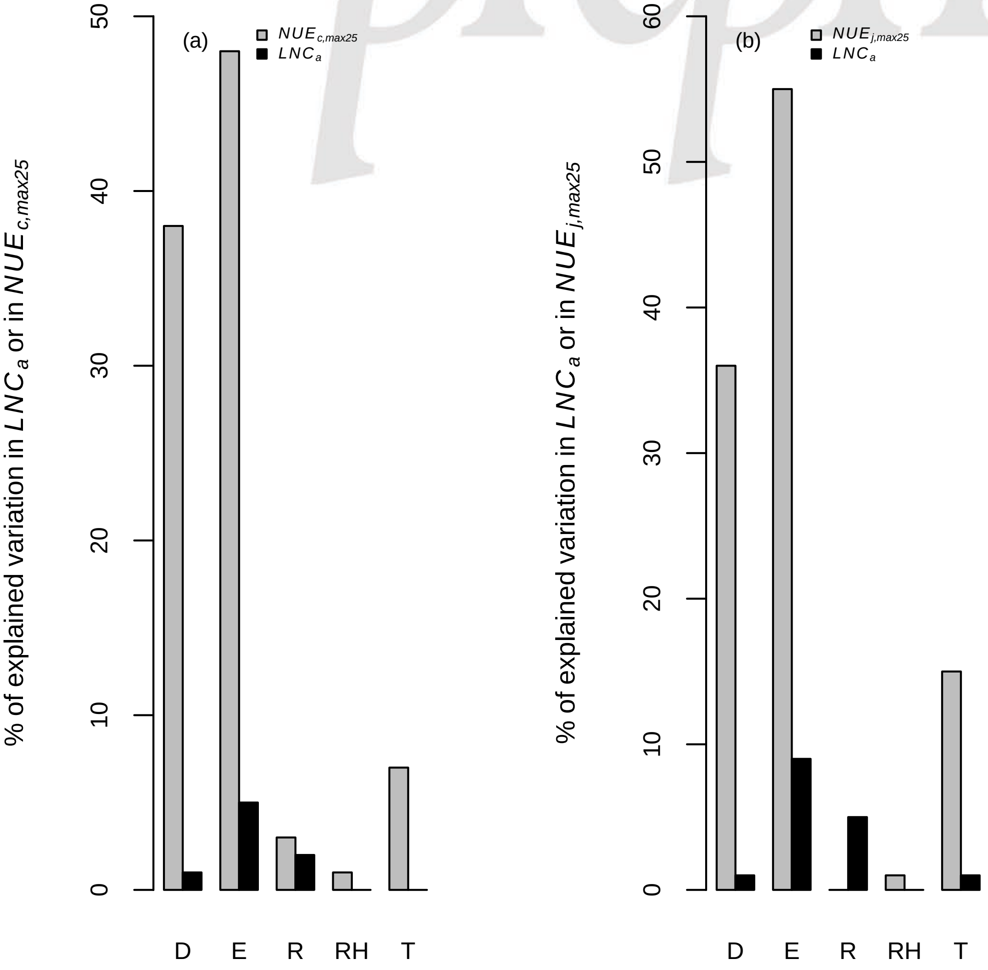

(a)
% of explained variation in $V_{c,max25}$
0
10
20
30
40
50
E
D
R
T
RH
$\tilde{E}$
LNC_a
(b) 5.27(<0.01)
$V_{c,max25}$ (μmol CO_2 m^{-2} s^{-1})
0
50
100
200
10
12
14
16
18
20
22
24
Day length (hrs)
(c) 0.05(<0.01)
0
100
200
300
400
500
Daytime Radiation (W m^{-2})
(d) −0.73(<0.05)
10
15
20
25
30
Growth Temperature (°C)
(e) 17.58(0.3)
0.3
0.4
0.5
0.6
0.7
0.8
Relative Humidity (unitless)
(f) 17.76(<0.01)
1
2
3
4
5
LNC_a (gN m^{-2})

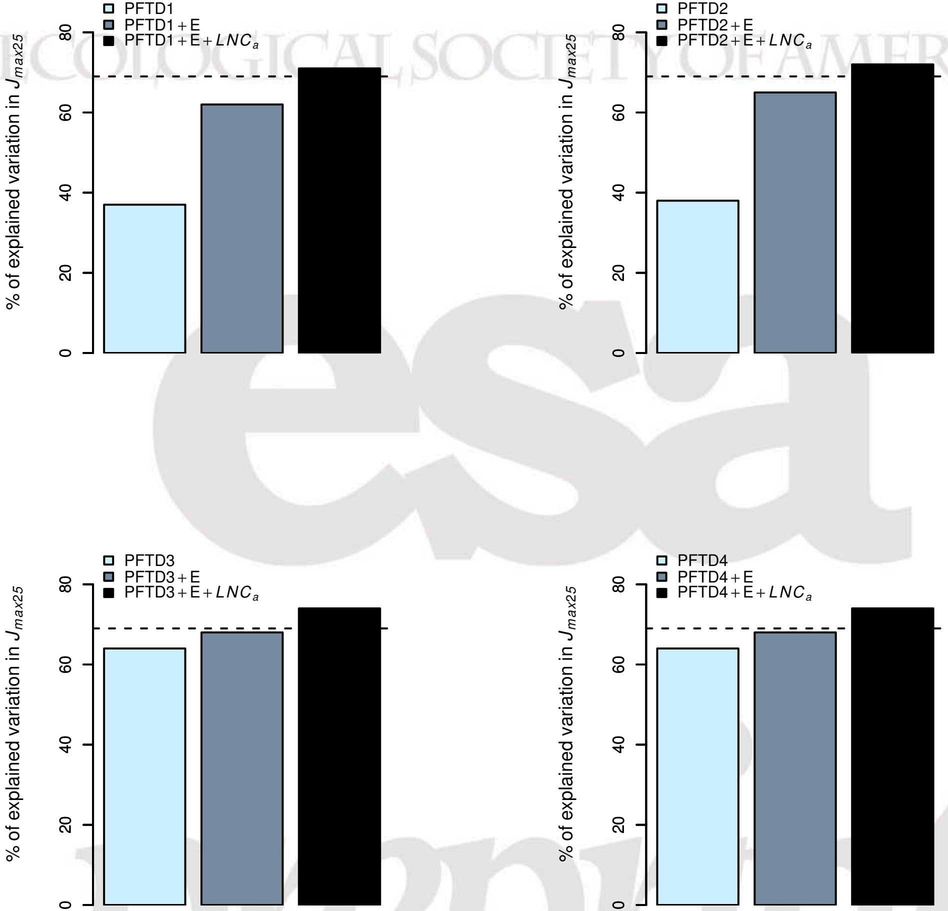

(a)
% of explained variation in J_{max25}
0
10
30
50
E
T
D
RH
R
Ẽ
LNC_a
(b) 12.54(<0.01)
J_{max25} (μmol electron m^{-2} s^{-1})
Day length (hrs)
(c) −3.24(<0.01)
Growth Temperature (°C)
(d) 52.91(0.09)
Relative Humidity (unitless)
(e) 0.08(<0.01)
Daytime Radiation (W m^{-2})
(f) 35.8(<0.01)
LNC_a (gN m^{-2})
0
100
300
500
10
12
14
16
18
20
22
24
15
20
25
30
0.3
0.4
0.5
0.6
0.7
0.8
200
400
1
2
3
4


(a)
$NUE_{c,max25}$
LNC_a
% of explained variation in LNC_a or $NUE_{c,max25}$
0
10
20
30
40
50
60
TRF1
TRF2
TRF3
TRF4
(b)
$NUE_{j,max25}$
LNC_a
% of explained variation in LNC_a or $NUE_{j,max25}$
0
10
30
50
70
TRF1
TRF2
TRF3
TRF4


(a)
☐ $NUE_{c,max25}$
■ LNC_a
% of explained variation in LNC_a or in $NUE_{c,max25}$
0
10
20
30
40
50
D
E
R
RH
T
(b)
☐ $NUE_{j,max25}$
■ LNC_a
% of explained variation in LNC_a or in $NUE_{j,max25}$
0
10
20
30
40
50
60
D
E
R
RH
T


(a)
☐ $E + LNC_a$
■ $PFTD4$
% of explained variation in $V_{c,max25}$
0
20
40
60
80
TRF1
TRF2
TRF3
TRF4
(b)
☐ $E + LNC_a$
■ $PFTD4$
% of explained variation in J_{max25}
0
20
40
60
80
TRF1
TRF2
TRF3
TRF4


(a)
$NUE_{c,max25}$
LNC_a
% of explained variation in LNC_a or in $NUE_{c,max25}$
0
10
20
30
40
50
D
E
R
RH
T
(b)
$NUE_{j,max25}$
LNC_a
% of explained variation in LNC_a or in $NUE_{j,max25}$
0
10
20
30
40
50
60
D
E
R
RH
T


PFTD1
PFTD1 + E
PFTD1 + E + LNC_a
PFTD2
PFTD2 + E
PFTD2 + E + LNC_a
PFTD3
PFTD3 + E
PFTD3 + E + LNC_a
PFTD4
PFTD4 + E
PFTD4 + E + LNC_a
% of explained variation in J_{max25}
0
20
40
60
80