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The impact of alternative V_{cmax} trait-scaling hypotheses on global gross primary production

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Summary	200
Introduction	823
Methods	2206
Results	1555
Discussion	2309
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Summary

- The maximum carboxylation rate of photosynthesis (V_{cmax}) is an influential plant trait that has multiple scaling hypotheses, which is a source of uncertainty in predictive understanding of global gross primary production (GPP).
- Four trait-scaling hypotheses (plant functional type, nutrient limitation, environmental filtering, and plant plasticity) with nine specific implementations are used to predict global V_{cmax} distributions and their impact on global GPP in the Sheffield Dynamic Global Vegetation Model.
- Global GPP varied from 108.1 to 128.2 PgC y^{-1}, 65 % the range of a recent model intercomparison of global GPP. The variation in GPP propagated through to a 27% coefficient of variation in net biome productivity (NBP). All hypotheses produced global GPP highly correlated (r=0.85-0.91) with three proxies of global GPP.
- Plant functional type based nutrient limitation, underpinned by a core SDGVM hypothesis that plant nitrogen status is inversely related to increasing costs of N acquisition with increasing soil C, adequately reproduced global GPP distributions. Further improvement could be achieved with accurate representation of water sensitivity and agriculture in SDGVM. Mismatch between environmental filtering (the most data-driven hypothesis) and GPP suggested that greater effort is needed understand V_{cmax} variation in the field, particularly in northern latitudes.

Key Words:

Gross Primary Production, Modelling photosynthesis, Plant functional traits, Trait-based modelling, Terrestrial carbon cycle, Co-ordination hypothesis, DGVM, Assumption centred modelling

Introduction

Photosynthetic carbon assimilation is the largest flux in the global carbon cycle, and accurate future projections from terrestrial biosphere models (TBMs) rely upon accurate representations of photosynthesis. Rates of photosynthesis are most commonly simulated as the minimum carboxylation rate of two processes—the Calvin-Benson cycle and light activated electron transport—modelled using Michaelis-Menten principles of enzyme kinetics (Farquhar & Wong, 1984; Collatz *et al.*, 1991; Harley *et al.*, 1992; von Caemmerer, 2000). These two realised rates are sensitive to their respective maximum rates—the maximum carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}), and terrestrial carbon cycle models are highly sensitive to these parameters (Zaehle *et al.*, 2005; Bonan *et al.*, 2011; Sargsyan *et al.*, 2014; Rogers, 2014; Rogers *et al.*, 2017). Many methods are used across TBMs to calculate V_{cmax} and J_{max}, and these methods represent competing hypotheses, formally or informally posed, on how these influential plant traits scale geographically. The diversity of hypotheses potentially leads to large, and previously unquantified, variation in the simulation of global photosynthetic carbon assimilation and poses the broader scientific question: what are the primary drivers of global V_{cmax} scaling?

Plant functional traits consist of a wide range of measurable plant phenotypic (chemical, physiological, and structural) properties that convey information pertaining to some aspect of plant function, and thus are used to describe plant function and functional diversity. Correlations between functional traits have been used to define common axes of plant strategies (Grime, 1974; Craine *et al.*, 2002; Wright *et al.*, 2004; Reich, 2014) and discrete plant functional types (PFTs), designed to simplify the diversity of plant life within a tractable modelling framework (Woodward & Cramer, 1996; Smith *et al.*, 1998; Wullschleger *et al.*, 2014). The quantitative nature of plant functional traits lends their use to global simulation modelling, allowing functions that represent the multiple ecosystem processes encoded in TBMs to be parameterised using values of the relevant plant functional traits. Recently, much attention has been paid to acknowledging wider and continuous variation in plant functional traits within ecosystem modelling (van Bodegom *et al.*, 2012, 2014; Scheiter *et al.*, 2013; Pavlick *et al.*, 2013; Verheijen *et al.*, 2013; Fyllas *et al.*, 2014; Fisher *et al.*, 2015; Kueppers *et al.*, 2016). Modelling this trait variation requires spatial and temporal trait-scaling hypotheses that go beyond the implicit hypothesis for many traits in many TBMs—that traits scale discretely across, and are static within, a limited set of broadly defined PFTs.

In the current study, multiple competing trait-scaling hypotheses for V_{cmax} and their impacts on global patterns of gross primary production (GPP) are assessed within a common modelling framework (the Sheffield Dynamic Global Vegetation Model—SDGVM). Broadly defined, four V_{cmax} scaling hypotheses are investigated: 1) discrete PFT variation, 2) nutrient limitation, 3) environmental filtering, and 4) plant plasticity allowing acclimation to environment. As discribed above, discrete PFT variation, is an hypothesis designed to represent key features of global diversity in plant function within a tractable modelling framework.

In more detail, nutrient, specifically nitrogen (N), limitation is hypothesised to affect $V_{cmax,25}$ due to the high concentrations of the enzyme RuBisCO in leaves which makes up a large portion of whole plant N demand. Empirically, $V_{cmax,25}$ and photosynthetic rates correlate with leaf N (Field & Mooney, 1986; Wright *et al.*, 2004; Kattge *et al.*, 2009) and plant N uptake (Woodward & Smith, 1995). SDGVM incorporates the hypothesis that plant N status is based on the principle of costs associated with plant N uptake as soil C increases and across mycorhizal types (Read, 1991; Woodward *et al.*, 1995). This hypothesis has been expanded on by recent model development efforts (Fisher *et al.*, 2010; Brzostek *et al.*, 2014). The environmental filtering hypothesis states that adaptation to local environment is the primary determinant of $V_{cmax,25}$ scaling. In our study, a data driven approach was taken to represent environmental filtering of $V_{cmax,25}$ following Verheijen *et al.*, (2013). Plant plasticity, which allows acclimation to environment, is based on the hypothesis that the process of natural selection has created plants able to respond to their environment at shorter timescales (e.g. days to weeks). These plant centric methods tend to consider an optimality perspective whereby plants adjust V_{cmax} to maximise the difference between costs and benefits (Chen et al., 1993; Maire et al., 2012; Prentice et al., 2014).

Our aims were to quantify and understand the causes of variability across these various scaling hypotheses of: 1) global V_{cmax} distributions; 2) simulated global distributions of GPP; and 3) temporal trends in global GPP and subsequent impacts on net biome productivity, the simulations of which is the primary purpose of global TBMs. To evaluate the spatial patterns of global GPP predicted by the various methods to scale V_{cmax} we use a number of global GPP observation proxies: the Max Plank Institute (MPI) upscaled eddy-flux estimate of GPP (Jung et al., 2011); global solar induced fluorescence (SIF) from the GOME-2 instrument (Joiner et al., 2013, 2016), and the CASA model calibrated using SIF data.

Methods

The SDGVM was developed as a daily timestep, global biogeography and eco-physiology model (Woodward et al., 1995; Woodward & Lomas, 2004) to predict the primary biomes of Earth and their associated fluxes of carbon (C) and water in response to global change. SDGVM has been described and extensively evaluated at site and global scales (Woodward *et al.*, 1995; Cramer *et al.*, 2001; Woodward & Lomas, 2004; Picard *et al.*, 2005; Sitch *et al.*, 2008; Beer *et al.*, 2010; De Kauwe *et al.*, 2013, 2014; Friend *et al.*, 2014; Walker *et al.*, 2014b; Zaehle *et al.*, 2014), so here we provide a brief description of the model and the process simulation methods relevant to this paper.

In SDGVM, C and water cycles conserve mass, while canopy nitrogen (N) is simulated through an empirical relationship of N uptake to soil C (Woodward et al., 1995; Woodward & Lomas, 2004), based on the principle of costs associated with plant N uptake as soil C increases and across mycorhizal types (Read, 1991). During the application of SDGVM to the FACE model data synthesis (FACE-MDS; Walker et al., 2014b; Medlyn et al., 2015) it was observed that SDGVM had low $V_{cmax,25}$ values ($V_{cmax,25} = 11N_a$; where N_a is leaf N per unit leaf area) and that using realistic values of $V_{cmax,25}$ observed at the FACE sites led to over prediction of GPP. The default $V_{cmax,25}$ values in SDGVM were calibrated to compensate biases caused by the assumption that photosynthesis calculated at mean daily radiation can be scaled by daylength to calculate mean daily photosynthesis. This assumption over-estimates photosynthetic efficiency by effectively linearising the response of photosynthesis to light. We corrected this bias by developing a sub-daily downscaling of light and photosynthesis calculations to 10 time periods during a half-day (described in more detail in Notes S1). The sub-daily calculation of photosynthesis allowed realistic $V_{cmax,25}$ values to generate realistic values of GPP in the model. SDGVM scales $V_{cmax,25}$ and $J_{max,25}$ by water limitation and leaf age.

Due to their strong correlation, in this study we focus only on V_{cmax} scaling hypotheses and employ a single relationship of $V_{cmax,25}$ to $J_{max,25}$ (Walker *et al.*, 2014a):

$$J_{max,25} = eV_{cmax,25}^{0.890} \quad . \qquad (1)$$

Each V_{cmax} scaling hypothesis—PFT, nutrient limitation, environmental filtering, and plant plasticity—for V_{cmax} scaling described in the introduction was implemented in the

SDGVM in multiple ways drawn from a number of datasets, empirical relationships, and specific mathematical representations (see below and Table 1).

Static traits (static_PFT): Static values of $V_{cmax,25}$ were derived by taking PFT means (using SDGVM PFT definitions; see SI for specific values) from the TRY database (www.try-db.org; data accession on *16 Nov 2010*) augmented to include data from the sparsely represented tropics (described below). This augmented TRY database was also used to derive the trait-environment relationships and is described in detail below. Each trait observation was linked to a PFT based on information on growth form (shrub, grass, tree), leaf habit (deciduous/evergreen) and photosynthetic pathway (C_3/C_4) (Verheijen et al., 2013, 2015).

Nutrient limitation hypotheses: We employ five implemetations of the nutrient limitation hypothesis. First (Ntemp_global), the original version of SDGVM calculated V_{cmax} from the rate of N uptake (N_u) (Woodward & Smith, 1994, 1995). N_u was calculated as a function of soil C, N, and mean annual air temperature (for details see: Woodward *et al.*, 1995). We label the original SDGVM method according to the assumption that sets it apart from other nutrient limitation hypotheses, that N_u is a function of temperature.

In later versions of SDGVM, the temperature modifier of N_u was removed and canopy N was calculated using a globally uniform, empirical scalar on N_u (Woodward *et al.*, 1995; Woodward & Lomas, 2004). All of the remaining implementations of the nutrient limitation hypotheses use the temperature independent function of N_u and canopy N. The second nutrient limitation implementation (N_global) was:

$$V_{cmax,25} = e^{3.712} N_a^{0.650} \quad , \qquad (2)$$

where N_a is leaf N, was taken from Walker *et al.*, (2014a) and was implemented globally. Third (N_PFT), we used the PFT-specific, linear $V_{cmax,25}$ to N_a relationships derived by Kattge et al., (2009). Forth (N_oxisolPFT), to simulate an implicit P limitation, we used the N_PFT relationships but replaced the evergreen broadleaved PFT relationship with a relationship derived on P poor oxisols. Fifth (NP_global), to simulate a more explicit P limitation on $V_{cmax,25}$ a function of $V_{cmax,25}$ where P was influential in interaction with N derived from a database of field and lab grown plants (Walker *et al.*, 2014a), was also simulated:

$$V_{cmax,25} = e^{3.946} N_a^{\left[0.921 + 0.282 \ln\left(P_a\right)\right]} P_a^{0.121} \quad . \qquad (3)$$

To simulate leaf P concentration we used a global relationship to total soil P derived by Ordonez et al., (2009), and a global total soil P map (Yang et al., 2014).

Environmental filtering: Environmental filtering was represented by empirically deriving PFT specific trait-environment relationships (Environ_PFT) from the TRY database $V_{cmax,25}$ values at the accession date (Niinemets, 1999; Kattge et al., 2009) augmented by Verheijen et al., (2015) to include $V_{cmax,25}$ from the tropics (Deng *et al.*, 2004; Meir *et al.*, 2007; Domingues *et al.*, 2010; van de Weg *et al.*, 2011; Cernusak *et al.*, 2011; Azevedo & Marenco, 2012; Nascimento & Marenco, 2013) that were not well covered in the TRY database. Each species within the database was assigned to a PFT based on the specific SDGVM PFT definitions.

Based on the global coordinates of the trait data, each trait entry was associated to a set of environmental conditions—mean annual temperature, mean temperature of the warmest month, mean temperature of the warmest month, temperature difference of warmest month and coldest month, total annual precipitation, total precipitation in the driest quarter, fraction of total precipitation that falls in the driest quarter, mean annual relative humidity, total annual down-welling shortwave radiation—taken from the CRU-NCEP dataset (the same as used to run the model simulations). For each PFT, a multiple regression with forward selection was run to relate variation in $V_{cmax,25}$ to environmental drivers. To avoid correlation between explanatory variables, variables with a correlation over 0.7 were not used in the same regression model.

An empirical, linear decrease in $V_{cmax,25}$ with CO_2 using the formulation of Verheijen et al., (2015) was also included as part of the response to environment (see Notes S1 for the relationships). $V_{cmax,25}$ is calculated at the beginning of each year for each PFT on each gridsquare based on mean environmental conditions of the past year.

V_{cmax} data for C4 plants were only available for these trait-environment relationships. Therefore in the simulations for all hypotheses these relationships (or static values for static_PFT) were used to set $V_{cmax,25}$ and phosphoenolpyruvate carboxylase ($PepC_{25}$) activity in C4 plants.

Plant plasticity: We examined plant plastcity by using the co-ordination hypothesis (Co-ord_global), which states that plants adjust V_{cmax} such that the carboxylation limited rate of photosynthesis (w_c) equals the electron transport limited rate of photosynthesis (w_j) over mean environmental conditions, commonly considered those of the past month (Chen et al., 1993; Maire et al., 2012). Using the Harley et al., (1992) photosynthesis functions, the co-ordination hypothesis to find V_{cmax} requires solving the following function (see Notes S1 for derivation):

$$0 = V_{cmax}\left(4C_i + 8\Gamma_*\right)\left[1 + \left(\frac{\alpha_i \bar{Q}}{S_{t,j} e \left(V_{cmax}/S_{t,v}\right)^{0.890}}\right)^2\right]^{0.5} - \alpha_i \bar{Q}\left(C_i + K_m\right) \tag{4}$$

where C_i is the internal CO_2 partial pressure (Pa), Γ_* is the photorespiratory CO_2 compensation point (Pa), α_i is the intrinsic quantum efficiency of electron transport (mol e mol^{-1} absorbed photons), $\bar{Q}$ is the mean absorbed light intensity of the past month (μmolm^{-2}s^{-1}), $S_{t,j}$ and $S_{t,v}$ are the temperature scalars for $J_{max,25}$ and $V_{cmax,25}$ to scale to leaf-temperature from 25°C, e is the base of the natural logarithm, and K_m is the effective Michaelis-Menten half-saturation constant for carboxylation when accounting for oxygenation (Pa). The denominator in the squared term, $S_{t,j} e \left(V_{cmax}/S_{t,v}\right)^{0.890}$, represents J_{max} at the mean temperature of the last month calculated using Eq 1 and considering temperature scaling.

The leaf nitrogen utilisation for assimilation (LUNA) (Xu et al., 2012; Ali et al., 2016) hypothesis was also evaluated (LUNA_global). LUNA optimises leaf N investment in various photosynthetic functions—light capture, electron transport, carboxylation—to maximise daily net photosynthesis (assimilation – leaf respiration) given mean environmental conditions (Ali et al., 2016). The LUNA optimisation also satisfies empirical environmental constraints and the constraint of co-ordination of w_c and w_j. Thus LUNA is a combination of plant plasticity, nutrient limitation, and environmental filtering hypotheses.

In this study we use the mean environmental conditions of the past 30 days, consistent with the averaging used for the co-ordination hypothesis (Ali et al., 2016 use the previous 10 days).

Scaling of $V_{cmax,25}$ to leaf temperature: Being enzymatically controlled, at short timescales V_{cmax} is highly dependent on leaf temperature and is usually normalised to a reference temperature, commonly 25 ºC, adding the subscript 25 to the notation ($V_{cmax,25}$). Three methods used to scale $V_{cmax,25}$ to leaf temperature were investigated (Figure S1 and Notes S1 for more details): 1) a saturating exponential (the SDGVM model default, see below); 2) the Arrhenius equation modified for enzymatic loss of function at high temperatures as presented in Medlyn *et al.*, (2002); and 3) the modified Arrhenius with emprical acclimation of temperature optima to local environmental conditions (Kattge & Knorr, 2007).

Model Setup & Simulations

The model simulations were run using the CRU-NCEP meteorological dataset 1901-2012 (Le Quéré et al., 2014; Figures S2-S4). PFT distributions were assumed static throughout the whole simulation period and were derived from land cover (LC) maps provided by the ESA CCI project (www.esa-landcover-cci.org; Figures S5-S12). The PFT fractions were derived from the LC maps using the LC to PFT conversion described in Poulter et al., (2015), and adjusted to account for the separation of C3 and C4 species that cannot be detected using MERIS wavebands (Poulter et al., 2015). The resultant PFT maps were then further categorised according to the SDGVM PFT classification.

Atmospheric CO_2 data were taken from the Scripps Ocean Institute merged ice-core and flask measurement global dataset (Keeling et al., 2005). The simulations were initialised with a 500 year spin-up that randomly selected meteorological years from the period 1901-1920. A separate spin-up was conducted for each ensemble member. The ensemble consisted of the nine different trait based approaches to simulate V_{cmax} (Table 1) and a subset of these nine approaches—N_global, Co-ord_global, and LUNA_global—each run with the three temperature scaling assumptions, for a total of 17 simulations. N_global, N_PFT, Co-ord_global, and LUNA_global were chosen to combine with the three temperature scaling approaches to represent a range of methods, and to see how the temperature scaling assumptions interacted with the dynamic spatial-scaling plant plasticity hypotheses (i.e. Co-ord_global, and LUNA_global).

Evaluation datasets

The simulated spatial distributions of global GPP were used to evaluate the impacts of the various V_{cmax} simulation methods. No method exists to measure GPP directly at the global scale, all methods involve assumptions and models (Anav et al., 2015) that may introduce bias or non-independence from the SDGVM simulations. We therefore compared modelled spatial distributions of GPP to three global GPP proxies—the empirically up-scaled flux tower estimates of GPP from the Max Plank Institute (MPI; Beer *et al.*, 2010; Jung *et al.*, 2011); and two datsets based on GOME-2 solar induced fluorescence (SIF; Joiner et al., 2013, 2016).

The two SIF based methods differed in their scaling of SIF radiance ($Wm^{-2}sr^{-1}y^{-1}$) to GPP ($gC\ m^{-2}y^{-1}$). The first scaling method (SIF-CASA) scaled SIF using modelled GPP from the Carnegie Ames Stanford Approach (CASA) Global Fire Emissions Database version 3 (GFED 3) model (ven der Werf et al., 2010). CASA primarily determined the spatial variation in GPP while SIF determined the temporal variation: in each gridpoint monthly SIF data were normalised by the gridpoint mean and then multiplied by the gridpoint mean CASA-GFED GPP (Eq 5, SIF-CASA). The second scaling method (scaled-SIF) was intended to allow SIF to determine both temporal and spatial variation in GPP: SIF were annually integrated in each grid-cell, normalised by the global mean SIF ($\overline{SIF}$) and then multiplied by the global mean of the SIF-CASA dataset (Eq 6).

$$cSIF_{i,j,t} = \frac{\overline{CASA}_{i,j} . SIF_{i,j,t}}{\overline{SIF}_{i,j}} , \tag{5}$$

$$s\overline{SIF}_{i,j} = \frac{c\overline{SIF} . \overline{SIF}_{i,j}}{\overline{SIF}} , \tag{6}$$

where CASA is the CASA GPP; cSIF is the CASA scaled GPP; sSIF is the simply scaled-SIF, and subscripts are the gridpoint latitude, i; longitude, j; and time, t.

At the time of writing, SIF data were available for the period 2007-2012 and so for consistency we present analyses for all model output over the same period. A comparison of model results for the last full decade, 2001-2010, with 2007-2012 give quantitatively similar results. The MPI data were available only until 2011, but given the MPI data have little inter-annual variability (Kumar *et al.*, 2016) this was expected to have little effect.

GPP predicted by the trait-scaling hypotheses were compared against the three GPP proxies using standard deviation, correlation, and centered root mean square difference. Combining these metrics in polar co-ordinates allows comparison of gridded datasets against a reference. These plots are known as Taylor diagrams (Taylor, 2001). Datasets were also analysed using principle component analysis (PCA) to identify common principle axes of variation across the datasets. As well as hypotheses and GPP proxies, climate variables (temperature, precipitation, and short wave radiation—SWR) were included to investigate climatic influence in the spatial patterns. Datasets were mean centred and scaled by standard deviation to give *z*-scores before conducting the PCA. The R (R Core Development Team, 2011) package 'plotrix' (Lemon, 2006) was used to plot the Taylor diagrams and the function 'prcomp' from the 'stats' package to perform the PCA.

Results

Global $V_{cmax,25}$ distributions

Global distributions of top-leaf $V_{cmax,25}$ predicted by the various trait scaling assumptions had markedly different means, variances, and latitudinal distributions (Figure 1 and S13). All but one (Ntemp_global) nutrient limitation hypothesis including LUNA_global (which is constrained by nutrient limitation) predicted relatively low variance in global $V_{cmax,25}$; with moderate values in the tropics, high values in the temperate zone, highest values in dry temperate regions, and lowest values in the Boreal zone before increasing in the high Arctic (Figure 1). The exception (Ntemp_global) showed relatively high $V_{cmax,25}$ variance with the highest values in the tropics that broadly decrease with latitude. Inclusion of phosphorus (P), either implicitly (N_oxisolPFT; Kattge et al., 2009) for the evergreen broadleaf PFT in the simulation, or explicitly (NP_global; Walker et al., 2014a), reduced $V_{cmax,25}$ marginally in much of the tropics (compared with N_PFT and N_global respectively).

In contrast, non-nutrient based hypotheses (Static_PFT, Environ_PFT, and Co-ord_global) tended to show the opposite pattern (Figure 1 and S13): more pronounced maximum $V_{cmax,25}$ values in northern cool wet areas dominated by green needle-leaf PFTs (Scandinavia and the North-American Pacific coast) and dry areas dominated by C3 grasses (the North-American west and Central Asia). The static_PFT values and the Environ_PFT relationships were derived from the same $V_{cmax,25}$ dataset. Therefore the observed similar latitudinal pattern was expected, as was the more spatially homogenous distribution for the static values per PFT. The co-ordination hypothesis is independent of the datasets used to produce the static_PFT and Environ_PFT, and produces highest $V_{cmax,25}$ values in the coldest and driest regions—north-eastern Canada and Asia, and the Himalayan plateau.

Consequences for the simulated Carbon Cycle

Across the nine $V_{cmax,25}$ scaling implementations, global mean annual GPP for the period 2007-2012 ranged from 108.1 to 128.2 PgC y^{-1} (Figure 2; Table 2). The ensemble mean ±s.d. annual GPP was 118.7±6.4 PgC y^{-1}, giving a coefficient of variation of 5.4 % (Table 2). The variation was somewhat higher for vegetation and soil carbon stocks (12.0 % and 13.9 %). Most crucially for carbon sequestration from the atmosphere under global change was that net biome productivity (NBP) varied by 27.1 % across the hypotheses tested.

The highest global GPP was simulated by the Ntemp_global implementation of nutrient limitation, closely followed by the static PFT hypothesis at 127.8 PgC y^{-1}. The global and PFT specific relationships of $V_{cmax,25}$ to leaf nitrogen simulated global GPP of 121.7 and 116.5 PgC y^{-1}. The inclusion of P as an additional limiting factor resulted in lower global GPP by 3.7 and 5.9 PgC y^{-1} respectively than consideration of N limitation alone. The P related drop in GPP was a result of disproportionate GPP reduction by P in generally high productivity regions, i.e. the tropics (Figure 2 and S14). Environmental filtering (Environ_PFT) and plant placticity (Co-ord_global) simulated similar mean GPP at 118.1 and 119.2 PgC y^{-1}. The constrained optimisation of functional leaf N allocation (LUNA hypothesis) yielded the lowest GPP at 108.1 PgC y^{-1}.

For a subset of $V_{cmax,25}$ scaling hypotheses (N_global, LUNA_global, Co-ord_global), the more up-to-date modified Arrhenius temperature scaling (Medlyn et al., 2002; Kattge & Knorr, 2007) were used, both with and without acclimation of temperature optima to growth temperature. Using these temperature scaling functions generally increased global GPP (Figure S15), especially for the co-ordination hypothesis (119.1-131.2 PgC y^{-1}). The increase in GPP for was primarily due to increasing GPP in the northern temperate and Boreal zones (Figure 3).

The hypotheses and their implementations also influenced the temporal trend in GPP (1900-2012) in response to increasing CO_2 and changing climate (Figure 4a). Ntemp_global resulted in the strongest change in GPP over the 20th century, the result of increasing temperatures stimulating N uptake. The LUNA hypothesis and the co-ordination hypothesis both predict shallower trajectories in GPP than any of the other scaling hypotheses. Scaling $V_{cmax,25}$ and $J_{max,25}$ using the modified Arrhenius function with and without temperature acclimation made little difference to the relative trajectories of GPP when used in conjunction with N_global, co-ordination, and LUNA hypotheses (Figure S16). Across the ensemble, NBP over the period 2007-2012 was strongly related to the change in global GPP over the time period 1901-2012 (Figure 4b).

Evaluating spatial distributions of GPP

Overlying the general, climatically driven spatial distribution of GPP, the differences in the spatial distributions of $V_{cmax,25}$ are observable in the simulated GPP distributions (Figure

2 and S3). To evaluate the various hypotheses, their global GPP predictions (mean annual GPP over 2007-2012) are compared in Taylor space (Figure 5 and Table S1) with several GPP proxies (MPI, scaled-SIF, SIF-CASA; Figure 2 and S17). No matter which GPP proxy was taken as reference, all hypotheses clustered closely in Taylor space with correlation c. r=0.9 (r=0.85-0.91), standard deviation within ±25% (with the exception of Ntemp_global when compared against both SIF based proxies and LUNA compared against MPI), and centred RMSD between 250 and 500 gC $m^{-2}y^{-1}$. All hypotheses were marginally less correlated to the scaled-SIF data (r=0.85-0.89) than the other two GPP proxies.

The most correlated hypotheses to MPI and SIF-CASA were N_global and N_PFT, though the improvements in these correlations were marginal (r=0.91 vs 0.88-0.90). Ntemp_global was generally less well correlated to all three proxies with substantially higher standard deviation and which predicted the highest global GPP and strongest latitudinal gradient. The least correlated hypotheses to MPI were LUNA_global and Environ_PFT, though again only marginally. Environ_PFT was also less well correlated with both SIF based proxies. N_PFT and N_oxisolPFT were the most correlated to scaled-SIF, marginally better than LUNA and N_global. The variance in the correlation across the hypotheses was greater when hypotheses were compared against the scaled SIF proxy (Figure 5c).

Difference plots between modelled GPP and GPP proxies (Figure 6 and S18-S19) showed that the N_oxisolPFT implementation tended to perform well against all three proxies, though there were some substantial under-predictions in tropical forests when compared against MPI (Figure S18). However, tropical GPP was consistently under-predicted by many implementations when compared against MPI, particularly in the Amazon. Static values per PFT and Ntemp_global clearly showed the strongest mismatches with the GPP proxies. Environ_PFT performed poorly in northern latitudes, particularly Scandinavia, and southern China, where V_{cmax} was predicted to be higher than any other implementation (Figure 1). Co-ordination and LUNA performed well, but tended to over-predict in nothern latitudes when compared against N_PFT and N_oxisolPFT. Across all implementations, GPP was under-predicted in Europe, eastern North America, and India while GPP was over-predicted in grasslands, particularly in South America, western North America and sub-Saharan Africa.

When the alternative, more realistic modified Arrhenius temperature response hypotheses were implemented, mismatches with scaled-SIF were unaffected for LUNA_global, slightly worsened in N_global, N_PFT, and noticeably worsened for Co-ord_global (Figure 5d). Implemented within the LUNA model, the three different temperature scaling assumptions made little difference to global GPP, presumably because the N constraint in LUNA was strong and the optimisation allowed flexibility around temperature responses to find a similar maximum assimilation rate across temperature scaling assumptions.

The SIF-CASA, scaled-SIF and MPI proxies were generally more correlated to each other than to any of the V_{cmax} hypothesis implementations, but only marginally. Arguably the proxies were as dissimilar from each other as the better model hypotheses were from the proxies, making it difficult to provide a definitive conclusion about which specific implementation of the various hypotheses was closest to GPP observation proxies.

Principal component (PC) analysis (PCA) was used to identify the common patterns and areas of divergence across both the models and the GPP proxies, and the potential cimatic drivers of the commonalities and differences. PCA demonstrated that 82 % of the spatial variance across simulated GPP, GPP proxies, and climatic variables are explained by a single PC (Figure S20). All model assumptions are closely grouped with high loadings on PC1 (Figure 7a), i.e. all model predictions are positively correlated with the spatial pattern of the first PC (Figure 7c). Closely grouped to the models on PC1 are all observed GPP proxies, as well as precipitation. Short wave radiation (SWR) and temperature were less strongly correlated with PC1, though the correlation was also positive, suggesting that precipitation is the primary driver of the dominant global pattern in GPP.

PC2 accounted for c. 11 % of spatial variance and segregates SWR and temperature (both positively correlated to PC2) from the model implementations, GPP proxies, and precipitation (Figure 7d). The remaining PCs combined account for 7 % of the spatial variation in the data and it is these remaining PCs that demonstrate the main areas of divergence between V_{cmax} implementations and GPP proxies.

PC3 and PC4 account for 4 % of variation. Short wave radiation and modelled GPP were correlated with PC3 while the GPP proxies (MPI most strongly) and precipitation were anti-correlated. PC3 shows the regions where modelled GPP is stimulated by light (primarily in natural grasslands; blue areas Figure 7e) or restricted by low light (red areas). By contrast, the GPP proxies appear to be stimulated by precipitation (red areas) or restricted by low precipitation (blue areas). PC4 segregates both SIF proxies from precipitation. PC4 shows high values almost exclusively in the worlds major agricultural regions—the North American cornbelt, the Northeast and South regions of Brazil and the area surrounding São Paulo, Europe and the Russian bread basket, India, particularly north India, central eastern China, and even smaller agricultural regions such as the Indus valley in Pakistan and alongside the Rift Valley in East Africa.

Discussion

We tested a series of plausible trait-scaling hypotheses for $V_{cmax,25}$, many of which are implemented in terrestrial ecosystem models, and found that they led to substantial variability in SDGVM simulated global GPP. Mean annual GPP ranged across the implementations of the hypotheses from 108.1 to 128.2 PgC y^{-1} (mean 118.7±6.4 PgC y^{-1}). The range in global GPP demonstrates the large sensitivity of simulated GPP to $V_{cmax,25}$ and this range encompasses 65% of that from a set of three models run in coupled and uncoupled modes (1990-2009 mean annual GPP range of 130-161 PgC y^{-1}, mean 145.6±12.6 PgC y^{-1}; Anav *et al.*, 2015). The simulations used by Anav *et al.*, (2015) were drawn from two inter-comparison projects, each with their own protocols, which is likely to inflate the range of simulated GPP compared to the simulations presented in this study which share a single protocol. Thus variation in simulated GPP caused by $V_{cmax,25}$ trait scaling hypotheses likely represents a substantial source of variation in GPP across models, which is currently unaccounted for in model intercomparisons (e.g. Anav *et al.*, 2015).

Dynamic trait-scaling based on nutrient limitation, in which plant nutrient status is inversely related to the cost of N acquisition, performed better than other hypotheses when compared against three GPP observation proxies. PFT specific relationships of V_{cmax} to leaf N resulted in the best performance. Static trait values per PFT were not supported by this study. The better performance of nutrient limitation implementations was most apparent when compared against the scaled-SIF GPP proxy and we argue that this is a more independent, thus more robust, comparison.

Evaluation of V_{cmax} distributions

Discerning which is the most realistic trait-scaling hypotheses was non-trivial. Currently no independent, globally gridded estimates of $V_{cmax,25}$ distributions exist. Many regions in global V_{cmax} datasets are only sparsely represented and one of the most comprehensive global V_{cmax} datasets was employed to compile the $V_{cmax,25}$ relationships to environment (Environ_PFT) for the trait filtering hypothesis (Kattge *et al.*, 2011; Verheijen *et al.*, 2013). The Environ_PFT prediction of the global $V_{cmax,25}$ distribution (Figure 1) is an empirical upscaling of $V_{cmax,25}$ point measurements using global climatic and land-cover information. Unlike other hypotheses tested, which additionally rely on either model process representation (e.g. simulation of leaf N) or more theoretical assumptions (e.g. co-ordination), Environ_PFT is data-driven and contingent only on the assumption that $V_{cmax,25}$ scales with environment (coefficient of determination 0.49-0.82 for C3 plants, see Notes S1; and Ali *et al.*, [2015]; Verheijen *et al.*, [2013]).

The data-driven Environ_PFT $V_{cmax,25}$ values are higher in northern latitudes relative to the tropics, as are $V_{cmax,25}$ distributions for the co-ordination hypothesis, which is in line with current literature (A. Rogers et al., unpublished). All the N based hypotheses in SDGVM (including LUNA) generally showed higher $V_{cmax,25}$ in the tropics than in the Boreal and Tundra zones (Figure 1) which is not consistent with our data-driven estimate (Environ_PFT). N limitation hypotheses predictions of tropical $V_{cmax,25}$ were consistent with the literature, often reported in the range 20-80 $\mu molm^{-2}s^{-1}$ (Domingues et al., 2010, 2015; Vårhammar et al., 2015; Norby et al., 2016), but were not consistent with values reported for the high Arctic, in the range 60-160 $\mu molm^{-2}s^{-1}$ (A. Rogers et al., unpublished).

The primary cause of the zonal $V_{cmax,25}$ distribution for the implementations constrained by N is the core SDGVM hypothesis that plant nutrient status is inversely related to soil carbon. This hypothesis is based on observations that plant N uptake decreases as dependence on organic N supply (correlated with mycorrhizal N supply) increases, which in turn is hypothesised a consequence of increasing soil organic matter (Read, 1991; Woodward et al., 1995). The global distributions of $V_{cmax,25}$ predicted by the nutrient limitation hypothesis are therefore generally the inverse of the distributions of soil carbon (Figure S21-S23), resulting in a broad latitudinal gradient in leaf N as soil decomposition rates slow with cooling temperatures. This cost-based hypothesis for plant N status reproduces the broad macro-ecological pattern of increasing N limitation as latitude increases suggested by leaf C:N and N:P stoichiometry (Reich & Oleksyn, 2004; McGroddy et al., 2004; Ordonez et al., 2009).

The original LUNA study at the global scale showed lower $V_{cmax,25}$ in the tropics and global distributions of top-leaf $V_{cmax,25}$ that were more similar to those predicted by Environ_PFT and Co-ord_global (Ali et al., 2016) than the N limitation hypotheses to which LUNA was more similar in this study. The defining difference is that Ali et al., (2016) assumed a constant top-leaf N of 2 gm^{-2}, while in SDGVM leaf N varies as a function of soil carbon. The results in SDGVM suggest that LUNA is more sensitive to variability in leaf N than to variability in environment.

Evaluation of GPP distributions

Principal components analysis (PCA) demonstrated that precipitation was the primary driver of the dominant mode of global GPP distributions in both the GPP proxies and all model simulations, and was therefore responsible for the strong correlation (0.85-0.91) of all hypotheses to the proxies. PCA indicated that the model simulations diverged from the observation proxies for two reasons: 1) a relative GPP stimulation by PAR in dry grasslands in SDGVM opposing a relative GPP reduction by low precipitation in the proxies (and *vice versa*; PC3); and 2) a relative stimulation of GPP in SIF based proxies in agricultural areas of the planet that was anti-correlated with precipitation and that was not apparent in the SDGVM nor MPI (PC4).

The stimulation of GPP by PAR without a counteracting reduction from low precipitation in SDGVM is most likely due to the relative insensitivity of SDGVM to low soil water avaialability when compared against other models (Medlyn *et al.*, 2016). On the other hand, the ubiquity of the under-prediction in all of Earth's major agricultural regions is likely due to agricultural improvement that was not represented by SDGVM—e.g. improved seed, fertilisation, and irrigation. The negative correlation of precipitation to PC4 and positive SIF proxy correlation in these agricultural areas (Figure 7) demonstrates the independence of GPP from precipitation in these regions., perhaps This independence implies that irrigation may be the primary driver of the under-prediction of GPP while recognising that irrigation levels are highly heterogeneous within these regions (Siebert et al., 2010).

GPP proxies (MPI, SIF-CASA, and scaled-SIF) were as dissimilar to each other as the better performing hypotheses were to the proxies. PCA showed that the SIF based proxies had relatively higher GPP in dry, agricultural regions of the planet compared with MPI. Relatively higher SIF based GPP in cropland areas compared against MPI has been previously observed (Guanter et al., 2014). This dissimilarity indicates an uncertain constraint from observations.

SIF is linearly related to MPI estimates of GPP at the temporal and spatial scales typically simulated by global TEMs (Guanter *et al.*, 2014; Parazoo *et al.*, 2014). SIF accurately reproduces seasonality in GPP (Joiner et al., 2014), though the coefficients of the linear relationships between SIF and GPP may vary with vegetation type (Frankenberg et al., 2011; Guanter et al., 2012; Parazoo et al., 2014). By assuming that the scaled-SIF proxy follows the same linear relationship to GPP across all terrestrial ecosystems, systematic errors (epistemic uncertainties in the classification of Beven, [2016]) are likely in the scaled-SIF estimate of the global GPP distribution. However, it is also extremely likely that epistemic uncertainties are common in the system of global GPP estimation in the MPI dataset—eddy-covariance flux estimates of NEE, empirical flux partitioning to derive GPP, derivation of empirical relationships of GPP with climate variables, scaling of point estimated GPP using a gridded climate dataset. The scaled-SIF data are a relatively direct, global-scale signal from the photobiochemical photosynthetic pathway and their spatial distribution is entirely independent of the model output, in contrast with the MPI product and SIF-CASA, both of which use climate data in their calculation.

While the Environ_PFT had the most data-driven and thus what we believe to be more accurate $V_{cmax,25}$ distributions, Taylor plots (Figure 5) and difference plots (Figures 6, S7, and S8) showed that their relative global GPP distributions had a larger mismatch to GPP proxies than the N limitation implementations in the northern latitudes. This difference was most apparent when compared against scaled-SIF. The latitudinal gradient in leaf N generated by the nutrient limitation implementations, and thus $V_{cmax,25}$, redistributes global GPP towards the tropics compared with other hypotheses (Figure 2, 6 and S14), yielding global GPP distributions more similar to global GPP proxies.

The mismatch of the data-driven estimates of $V_{cmax,25}$ from Environ_PFT indicates latitudinal variability in the relationship of $V_{cmax,25}$ with GPP. The reason for this mismatch is unclear. SDGVM may over-predict LAI in northern latitudes, and it may be that lower V_{cmax} in nutrient limitation is compensating for high LAI. However, using a multi-scale state estimation procedure to combine GPP estimates from TEMs, SIF, and flux-towers; Parazoo et al., (2014) noted a redistribution of GPP from northern latitudes to the tropics in the optimised GPP state compared with the prior estimates from the TEMs. Similar decoupling between $V_{cmax,25}$ and GPP at high latitude has also been observed in preliminary simulations of the Community Land Model (CLM version 5.0) using satellite phenology (i.e. data-driven LAI), LUNA, and observed leaf N (Fisher, pers. Comm.). Alternatively, there may be insufficient V_{cmax} data for high-latuitude systems and normalising V_{cmax} to 25 °C in regions that experience these temperatures only in extreme cases and with generic temperature scaling functions could be introducing a bias in the V_{cmax} data.

Recent evidence has suggested that leaf phosphorus may modify, co-limit, or replace the $V_{cmax,25}$ to N relationship (Reich & Oleksyn, 2004; Domingues *et al.*, 2010; Walker *et al.*, 2014a; Norby *et al.*, 2016); though the physiological link to photosynthesis is more complex. Considering P limitation either implicitly (N_oxisolPFT) or explicitly (NP_global) did not clearly improve the fit to the GPP proxies (compared against their N only counterparts) based on the quantitative comparison. However, a visual comparison of the difference plots suggests that the N_oxisolPFT implementation produced the least over-all difference to GPP proxies, indicating perhaps a role for P limitation of photosynthesis in the tropics. A map of oxisols vs non-oxisols to segregate evergreen broadleaved PFTs would likely improve the simulation.

GPP trend and NBP

Most importantly for projections of the global carbon cycle under environmental change, the response of GPP to global change (1901-2012) across the V_{cmax} hypotheses was different, with plant-centric acclimation hypotheses showing a lower response of GPP to increasing CO_2. NBP variability over 2007-2012 was strongly related to the change in GPP over the 20th century and the 5.4% coefficient of variation in GPP to propagate through to 29% variation in NBP.

Projecting the trajectory of land carbon uptake is the major purpose of global terrestrial ecosystem models and the 'acclimation' of $V_{cmax,25}$ to increasing CO_2, and perhaps other factors of global change, predicted by these hypotheses has consequences for the projected terrestrial carbon sink. Consequences we cannot currently evaluate with data due to the difficulty in measuring GPP and terrestrial NBP, especially the 20th century trends; though coupled Earth-System models are thought to under-estimate the global carbon sink (Hoffman et al., 2014).

Co-ord_global and LUNA_global predict the shallowest, and almost indentical, GPP trends over the 20th century (Figure 4a). The co-ordination hypothesis (also embedded within LUNA) restricts CO_2 fertilisation of GPP to the effect of CO_2 on light-limited photosynthesis.

Assuming all else is equal, increasing CO_2 increases both the carboxylation limited photosynthetic rate, w_c, and the electron transport limited rate, w_j, but w_c is increased in greater proportion (the degree of which is dependent on the choice of model for w_j). Thus co-ordination reduces $V_{cmax,25}$ at the higher CO_2 concentration to balance w_c with w_j. Thus, under co-ordination, the CO_2 fertilisation of GPP is primarily driven by the CO_2 response of light-limited photosynthesis, which is lower than the CO_2 response of carboxylation limited photosynthesis. The decline in V_{cmax} driven by the co-ordination hypothesis is stronger than the decline in Environ_PFT (Figure S24) which was the only hypothesis to have an explicit reduction of V_{cmax} in response to CO_2. We assumed a fixed relationship between J_{max} and V_{cmax} for the implementation of co-ordination in this analysis (Eq 5). Given that these plant plasticity hypotheses are founded within the concept of optimality (Xu *et al.*, 2012; Prentice *et al.*, 2014; Wang *et al.*, 2014), the restriction of the CO_2 response to the smaller electron transport (light) limited under co-ordination suggests that the optimal solution would include a variable response of the J_{max} to V_{cmax} relationship to changing CO_2 concentration.

In summary, the analysis of multiple V_{cmax} trait scaling hypotheses on simulated GPP suggested that nutrient limitation was the more likely driver of global V_{cmax} distributions. N limitation was implemented via a relationship of decreasing leaf N with increasing soil C based on increasing costs of N uptake. Of the nutrient limitation implementations, the PFT specific relationships to leaf N that implicitly accounted for P limitation in broadleaved evergreens (Noxisol_PFT; Kattge *et al.*, 2009) were found to most closely match the GPP proxies. Incorporating a global map of oxisols would likely help to further refine this implementation. For SDGVM and other global carbon cycle models we recommend the Noxisol_PFT relationships to leaf N, particularly for models that can simulate N cycling or spatially dynamic leaf N. For carbon-cycle only models, the static_PFT hypothesis did not reproduce spatial distributions of global GPP as well and we suggest that the scaled relationship of N uptake to soil C (Woodward *et al.*, 1995) without the temperature modifier could be a relatively straight forward way to implement dynamic leaf N allowing the use of the Noxisol_PFT relationships. These recommendations are contingent on the GPP proxies used, which are uncertain. We suggest that further measurements of V_{cmax} in Boreal and Arctic ecosystems, that include the V_{cmax} response to temperature in these ecosystems, will help to discriminate among alternate hypotheses.

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Author contributions

All authors contributed to the writing of the manuscript. APW conceived of the study, ran the model, analysed the data, and led the writing. APW, ML, FIW, TQ made additional developments to the SDGVM. CX contirbuted to adding the LUNA hypothesis to SDGVM. PvB derived the trait environment relationships. XY contributed the soil P dataset. JJ contributed SIF data. NM derived the land-cover datasets. MDK and TK contributed to the analysis.

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Figure Captions

Figure 1. Mean growing season top-leaf $V_{cmax,25}$ (μmol $m^{-2}s^{-1}$) over the period 2007-2012 for the nine implementations of the four V_{cmax} trait-scaling hypotheses. Growing season defined as periods during which LAI was greater than one. Values are reported prior to scaling of V_{cmax} by water-stress or leaf-age.

Figure 2. Mean annual GPP GPP (gC $m^{-2}y^{-1}$) for the period 2007-2012 for the nine implementations of the four V_{cmax} trait-scaling hypotheses and the three global GPP proxies. Global mean annual GPP shown in each panel (PgC).

Figure 3. Mean annual zonal GPP (PgC) over the period 2007-2012 for three of the V_{cmax} trait-scaling implementations in combination with the three temperature scaling assumptions.

Figure 4. Variability in GPP trends and NBP for the nine implementations of the four V_{cmax} trait-scaling hypotheses. (a) Trends in the absoute change in global GPP over the period 1901-2012; and (b) the relationship between mean annual NBP 2007-2012 and the change in GPP 1901-2012 across the nine hypotheses.

Figure 5. Taylor plots of GPP (2007-2012) for the nine implementations of the four V_{cmax} trait-scaling hypotheses compared against the three GPP proxies: (a) MPI, (b) SIF-CASA, (c) scaled-SIF; annd (d) including the two additional temperature scaling hypotheses (modA and tacc) for N_global, N_PFT, LUNA_global and co-ord_global. Taylor plots compare datasets against a reference dataset using correlation (grey radial isolines), standard deviation (blue circular isolines, zero at the origin), and root mean difference (green circular isolines, zero at the reference dataset on the x-axis).

Figure 6. Difference plot of GPP simulated by the nine implementations of the four V_{cmax} trait-scaling hypotheses minus the scaled-SIF GPP proxy.

Figure 7. Principle components analysis of the nine implementations of the four V_{cmax} trait-scaling hypotheses with the three GPP proxies and three climatic variables: precipitation, temperature, and short-wave radiation. Loadings of variables on (a) PC1 and PC2, (b) PC3 and PC4; maps of (c) PC1 pattern (d) PC2 pattern (e) PC3 pattern, and (f) PC4 pattern. Break points on the colour scale are at quantiles (0.025, 0.1, 0.2, 0.35, 0.65, 0.8, 0.9, 0.975) in the gridpoint scores on each PC to give even representation of the data.

Table 1. Summary of $V_{cmax,25}$ and V_{cmax} temperature scaling hypotheses.

Hypothesis	Label	Specific method	PFT specific	Description	Reference	Papers/Models	Dataset
Static	static_PFT	Static	Y	Augmented TRY database means	Verheijen et al., 2015	Most CMIP5 models	Literature search augmented TRY
Nutrient limitation	Ntemp_global	empirical f(Nu)	N		Woodward et al., 1995	Original SDGVM	Woodward et al., 1995
	N_global	empirical f(Na)	N	Power law	Walker et al., 2014		Literature search Walker et al., 2014
	NP_global	empirical f(Na,Pa)	N	Power law including leaf phosphorus	Walker et al., 2014		Literature search Walker et al., 2014
	N_PFT	empirical f(Na)	Y	Linear from TRY database	Kattge et al., 2009	O-CN, other N cycle models,	TRY
	N_oxisolPFT	empirical f(Na)	Y	As above but with oxisol relationship for evergreen broadleaf PFT	Kattge et al., 2009		TRY
Environmental filtering	Environ_PFT	empirical f(env.)	Y	Augmented TRY relationship to …	Verheijen et al., 2015		Literature search augmented TRY
Plant plasticity	Co-ord_global	Theoretical f(Q, T, VDP)	N	Vcmax adjusted so wc = wj given mean environment over the past 30 days	Chen et al., 1993; Maire et al., 2012	First principles Wang et al	na
Plant plasticity & nutrient limitation	LUNA_global	4. Theoretical f(Na, Q, T, RH)	N	Constrained optimisation of leaf N allocation given mean environment over the past 30 days	Xu et al., 2012; Ali et al., 2016	CLM5.0	Literature search Ali et al., 2015
	Temperature scaling						
Static	*	SDGVM default	N	Saturating exponential		SDGVM	
Static	*_modA	Modified Arrhenius	Y	Temperature optimum	Medlyn et al., 2002		
Plant plasticity	*_tacc	Modified Arrhenius with acclimation	Y (modA only)	Temperature optimum varies with growth temperature	Kattge & Knorr, 2007		

Nu—N uptake, Na—N per unit leaf area, Pa—P per unit leaf area, Q—incident PAR per unit leaf area, T—leaf temperature, VPD—vapour pressure deficit, RH—relative humidity. *

represents the label for one of four Vcmax scaling hypotheses (N_global, N_PFT, LUNA_global, or Co-ord_global) used in conjunction with these three temperature scaling hypotheses.

Table 2. Carbon cycle variables for the nine Vcmax scaling hypotheses (means over the period 2007-2012). Net primary productivity, NPP; soil carbon stocks, Csoil; vegetation carbon stocks, Cveg; total terrestrial carbon stocks, Ctotal; standard deviation, sd; coefficient of variation, CV. All variables are in gC m^{-2} y^{-1}.

	GPP	NPP	NBP	Csoil	Cveg	Ctotal
static_PFT	127.8	73.4	1.7	1619.8	777.7	2397.5
Ntemp_global	128.2	71.1	2.9	1009.5	768.0	1777.5
N_global	121.7	66.8	2.1	1304.6	680.9	1985.5
N_PFT	116.5	64.9	1.9	1285.6	581.8	1867.4
N_oxisolPFT	110.6	62.5	1.6	1270.9	517.4	1788.3
NP_global	118.0	64.1	1.9	1289.6	694.2	1983.8
LUNA_global	108.1	60.9	1.2	1349.2	558.4	1907.7
environ_PFT	118.1	66.2	1.9	1253.1	781.2	2034.3
co-ord_global	119.3	69.6	1.1	1494.9	714.3	2209.2
mean	**118.7**	**66.6**	**1.8**	**1319.7**	**674.9**	**1994.6**
sd	**6.4**	**3.9**	**0.5**	**158.8**	**94.0**	**189.6**
CV (%)	**5.4**	**5.8**	**27.3**	**12.0**	**13.9**	**9.5**

Supplemental Material

Figure S1. Temperature responses of Vcmax.

Figure S2-S4. Climate data used to run the model.

Figure S5-S12. Land-cover data used to run the model.

Figure S13. Zonal plot of $V_{cmax,25}$.

Figure S14. Zonal plot of GPP.

Figure S15. Global GPP for various V_{cmax} temperature scaling assumptions.

Figure S16. 20th and 21st change in GPP for various V_{cmax} temperature scaling assumptions.

Figure S17. GPP observation proxies.

Figure S18. Difference plot of model GPP to MPI GPP proxy.

Figure S19. Difference plot of model GPP to SIF-CASA GPP proxy.

Figure S20. Variance explained by each principal component.

Figure S21-S23. Modelled relationships between leaf N and $V_{cmax,25}$ with soil carbon.

Figure S24. 20th and 21st change in modelled $V_{cmax,25}$.

Figure S25. 20th and 21st change in modelled LAI.

Notes S1. Additional methods description.

Table S1. Metrics for Taylor plots.