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# Impacts of trait variation through observed trait-climate relationships on performance of a representative Earth System model: a conceptual analysis

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18907

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Received: 12 October 2012 – Accepted: 7 December 2012 – Published: 19 December 2012

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Published by Copernicus Publications on behalf of the European Geosciences Union.

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Abstract

In current dynamic global vegetation models (DGVMs), including those incorporated into Earth System Models (ESMs), terrestrial vegetation is represented by a small number of plant functional types (PFTs), each with fixed properties irrespective of their predicted occurrence. This contrasts with natural vegetation, in which many plant traits vary systematically along geographic and environmental gradients. In the JS-BACH DGVM, which is part of the MPI-ESM, we allowed three traits (specific leaf area (SLA), maximum carboxylation rate at 25 °C ( $V_{\text{cmax}_{25}}$ ) and maximum electron transport rate ( $J_{\text{max}_{25}}$ )) to vary within PFTs via trait-climate relationships based on a large trait database. For all three traits, the means of observed natural trait values strongly deviated from values used in the default model, with mean differences of 32.3 % for  $V_{\text{cmax}_{25}}$ , 26.8 % for  $J_{\text{max}_{25}}$  and 17.3 % for SLA. Compared to the default simulation, allowing trait variation within PFTs resulted in GPP differences up to 50 % in the tropics, in > 35 % different dominant vegetation cover, and a closer match with a natural vegetation map. The discrepancy between default trait values and natural trait variation, combined with the substantial changes in simulated vegetation properties, together emphasize that incorporating observational data based on the ecological concepts of environmental filtering will improve the modeling of vegetation behavior in DGVMs and as such will enable more reliable projections in unknown climates.

## 1 Introduction

Terrestrial vegetation plays a pivotal role in land-atmosphere interactions, modifying carbon, water and heat fluxes via biochemical processes such as photosynthesis and respiration or via biophysical vegetation properties such as stomatal conductance and albedo. Therefore, a correct representation of terrestrial vegetation and its dynamics in Earth System Models (ESMs) is essential, especially for future climate projections. For this purpose, Dynamic Global Vegetation Models (DGVMs) were developed. DGVMs

**BGD**

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



integrate vegetation dynamics with land surface models to allow analysis of transient vegetation responses and feedbacks to climate (Foley et al., 1998; Prentice et al., 2007). Compared to earlier models, vegetation dynamics and interactions between the biosphere and atmosphere have been much improved over the past decade, although many issues still need to be resolved (Quillet et al., 2010).

One of these issues is the way in which Plant Functional Types (PFTs) are used to represent vegetation. PFTs are classes of plant species with presumably similar roles in an ecosystem, responding in a comparable manner to environmental conditions like water and nutrient availability (Harrison et al., 2010; Lavorel et al., 1997). They are defined by a combination of attributes such as plant growth form (e.g. trees, shrubs, grasses, herbs), phenology (evergreen, raingreen, summergreen) and bioclimatic tolerances (e.g. minimum temperature requirements). Notably, most current PFT classifications use constant parameter values for some key plant traits, i.e. plant properties that reflect the way plants cope with their environment (McGill et al., 2006; Violle et al., 2007). Using constant plant traits in PFTs has serious limitations (Harrison et al., 2010; Ordoñez et al., 2009; Van Bodegom et al., 2012), as it does not reflect the trait variation observed within and between communities (Ackerly and Cornwell, 2007; Freschet et al., 2011; Kooyman et al., 2010; Westoby et al., 2002), therefore not accounting for local environmental constraints. Furthermore, global trait database analyses have shown that the variation in plant traits is large within PFTs and often even greater than the difference in means among PFTs (Laughlin et al., 2010; Reich et al., 2007; Wright et al., 2005a). Even though PFTs may capture a significant part of the global plant trait variation, a large part (for some traits up to 75 %) may still be unexplained (Kattge et al., 2011) and is thus not represented in current DGVMs.

Given that plants can adjust to the environment via changes in traits, and that such changes influence ecosystem functioning (Diaz et al., 2004; Eviner and Chapin, 2003; Lavorel and Garnier, 2002), implementing these trait-driven interactions within PFTs of DGVMs is highly relevant. By simulating the variation in plant responses one allows plant to adapt to climate and plant-atmosphere feedbacks to occur, which in current

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



models is only possible through shifts in PFT-abundances (Van Bodegom et al., 2012). While in some DGVMs, trait variation has been incorporated to enable modeling of nutrient cycles (Gerber et al., 2010; Zaehle and Friend, 2010) or was allowed via stochastic processes (Alton, 2011), these methods only partly describe the drivers and ranges of the prevailing trait variation.

An alternative way to capture and predict trait variation in DGVMs is to include the relationships between natural trait variation and their multiple environmental drivers. At both regional and global scales traits are related to large scale environmental gradients of, for instance, temperature, water and nutrient availability or disturbances (Ordoñez et al., 2009; Van Ommen Kloeke et al., 2012; Wright et al., 2005b). Such relationships between environmental conditions and traits can potentially be understood via ecological assembly theory, which describe the processes that determine species assemblages (Cornwell and Ackerly, 2009; Cornwell et al., 2006; Götzenberger et al., 2012). An important abiotic assembly process is habitat filtering (Keddy, 1992), which describes how local environmental drivers (e.g. soil fertility or precipitation) constrain the range of potential species and related trait values in a given habitat. For many traits, such as specific leaf area, leaf nitrogen and wood density this may contribute to trait convergence within communities (Freschet et al., 2011; Swenson and Enquist, 2007), resulting in global relationships between community trait means and climatic drivers. By identifying the environmental drivers of variation in site trait means, multiple causes of variation are determined and the observed natural trait variation can be modeled with a high level of accuracy.

The aim of this study is thus to improve the modeling of vegetation responses and enable vegetation-atmosphere feedbacks in DGVMs by incorporating climate-driven trait variation within PFTs, based on large observational trait databases. So far observational trait data have been used to derive mean parameter values and uncertainties for PFTs in the context of different vegetation models (Kattge et al., 2009; Ziehn et al., 2011), but this study provides the first concept (to our knowledge) to predict mean

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



parameter values per PFT for each individual grid cell, based on a systematic analysis of observed trait-climate relationships.

These relationships were implemented in the JSBACH DGVM, which is part of the Max Planck Institute Earth System Model (MPI-ESM) (Brovkin et al., 2009; Raddatz et al., 2007; Roeckner et al., 2003). It is representative of most DGVMs currently used in the context of ESMs and used in carbon cycle model intercomparisons (Friedlingstein et al., 2006). We simulate variation in three originally constant and PFT-specific key leaf traits in JSBACH: specific leaf area (SLA), maximum carboxylation rate at a reference temperature of 25 °C ( $V_{\text{cmax}_{25}}$ ) and maximum electron transport rate at 25 °C ( $J_{\text{max}_{25}}$ ). To determine relationships between these three traits and climatic drivers for each PFT, data from the TRY global plant trait database (Kattge et al., 2011) were related to global climatic data. Based on these relationships between traits and climate, SLA,  $V_{\text{cmax}_{25}}$  and  $J_{\text{max}_{25}}$  were re-parameterized for each grid cell on a yearly basis, depending on the (local) climatic conditions in a grid cell. This enabled feedbacks between plants and environment, as traits within natural PFTs could vary dynamically in space and time. A simulation with variable traits is compared for trait distribution, productivity and vegetation distribution to a default simulation with the original trait values of the model, and to an additional simulation with constant, but observation-based, trait values.

As DGVMs are already parameterized to produce approximate realistic results, our variable traits simulation will not necessarily approach reality better than the default simulation. Therefore, in this paper the focus lies on simulation intercomparisons to evaluate the impact of incorporating climate-driven trait variation. A formal validation with observational data is not the primary aim of this paper, as the simulations are not meant to represent current vegetation or climate states, but instead are run into equilibrium states with their own internal climate and vegetation composition in order to study the impacts of trait variation within PFTs. Nevertheless, we include comparisons with global biomass and gross primary productivity (GPP) estimates and potential vegetation distribution to evaluate the realism of the various simulation results.

## BGD

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 2 Materials and methods

### 2.1 Model description

Simulations were performed with the ESM of the Max Planck Institute (MPI-ESM). The model setup consisted of the JSBACH DGVM, a land surface model (Raddatz et al., 2007) with a vegetation dynamics module (Brovkin et al., 2009), coupled to the atmosphere model ECHAM5 (Roeckner et al., 2003) to allow for vegetation-atmosphere feedbacks. The model version on spatial resolution of T63 (approx.  $1.875^\circ$ , dividing the world into 18432 grid cells) with 47 atmospheric layers was used, with atmospheric  $\text{CO}_2$  concentration kept constant at 353.9 ppm. Seasonal sea surface temperatures and sea ice were prescribed from a default simulation with the MPI ocean model (MPI-OM) (Marsland et al., 2003). Vegetation dynamics were interactive to allow for vegetation shifts and vegetation-atmosphere feedbacks through trait dynamics. Terrestrial grid cells contained multiple PFTs, each occupying a certain fraction, depending on their competitive ability (based on net primary productivity (NPP)). This study does not include crops and pastures, but focuses on responses of natural vegetation, represented by eight PFTs. These were tropical broadleaved evergreen trees (TrET), tropical broadleaved deciduous trees (TrDT), extra-tropical (both temperate and boreal) evergreen trees (ExTrET), extra-tropical deciduous trees (ExTrDT), raingreen shrubs (RgSh), cold/deciduous shrubs (DSh), C3-grasses (C3G) and C4-grasses (C4G). No anthropogenic land use or land cover change was simulated.

### 2.2 Selected trait and climate data

In JSBACH, SLA ( $\text{m}^2 \text{kg}^{-1}$  carbon) is related to the amount of carbon that can be stored in the green and reserve carbon pools.  $V_{\text{cmax}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $J_{\text{max}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) both control carbon assimilation.  $V_{\text{cmax}_{25}}$  also determines the reference respiration at  $25^\circ\text{C}$ . Observational data for these traits (see Table 1 for references) were obtained mainly from the TRY database (Kattge et al., 2011) with additional data

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



for SLA from the database by Van Bodegom et al. (2012) and for  $V_{\text{cmax}_{25}}$  and  $J_{\text{max}_{25}}$  from Domingues et al. (2010).

Only  $V_{\text{cmax}}$  and  $J_{\text{max}}$  standardized to a reference temperature of 25 °C were used. Most  $V_{\text{cmax}}$  and  $J_{\text{max}}$  values had already been standardized to this temperature via the formulation of the photosynthesis model by Farquhar et al. (1980) used in the context of JSBACH (Kattge and Knorr, 2007). For other records for which the temperature during measurement was recorded, standardization was done according to this formulation. For C4-grasses, variation in PEPcase  $\text{CO}_2$ -specificity ( $\text{PEP}$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ) instead of  $J_{\text{max}_{25}}$  was determined, following Collatz et al. (1992). Since for C4-grasses insufficient observational PEP and  $V_{\text{cmax}_{25}}$  data were available, these traits were estimated more indirectly applying insights from Simioni et al. (2004), who determined PEP and  $V_{\text{cmax}_{25}}$  based on leaf nitrogen (N) content ( $\text{g m}^{-2}$ ) (regressions based on two C4-species). Therefore, for C4 grasses, additional information on leaf N was obtained from the TRY database.

To link climate and trait data, only geo-referenced trait observations from field sampling and field experiments were used. PFT assignment of species was based on available data in the above mentioned databases on growth form (shrub, grass, tree), leaf habit (deciduous/evergreen) and photosynthetic pathway (C3/C4). The climatic domain of a species (tropical, boreal etc.) was determined based on the Köppen-Geiger climate classification (Kottek et al., 2006) and applied to the geo-referenced observations. This resulted in 12 394 observations for SLA distributed over 2869 species and 1052 (PFT-specific) sites, 761 observations over 129 species and 70 sites for  $V_{\text{cmax}_{25}}$  and 402 observations over 108 species and 56 sites for  $J_{\text{max}_{25}}$  (see supplementary material S1 for global map with locations of trait data).

Global climate data on mean annual precipitation ( $\text{MAP}$ ,  $\text{mm yr}^{-1}$ ), mean annual relative humidity (Reh, %), mean annual temperature ( $\text{MAT}$ , °C), mean temperature of coldest and warmest month ( $T_{\text{min}}$  and  $T_{\text{max}}$ , °C) were collected from a global 10 min gridded data set of mean monthly climate data based on weather stations from the Climatic Research Unit (CRU) (New et al., 2002). Net shortwave radiation ( $\text{NSWR}$ ,  $\text{W m}^{-2}$ ) was

## BGD

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





calculated based on distance to sun and percentage sunshine (from CRU) according to Allen et al. (1998) on a global 30 min spatial resolution. Soil moisture was taken from GLEAM, a methodology that estimates soil moisture and evapotranspiration based on remotely sensed data at a global 15 min spatial resolution (SoilMoist,  $\text{m}^3 \text{m}^{-3}$  for 1 m depth, Miralles et al., 2011). Soil moisture was the only edaphic control of trait variation, since soil N was not modeled in this version of JSBACH.

## 2.3 Trait-climate relationships

Given the lack of global quantitative deterministic predictions, the observed natural variation of SLA,  $V_{\text{max}_{25}}$  and  $J_{\text{max}_{25}}$  was described for each PFT by the simplest models possible, i.e. linear regressions. For this purpose, we used PFT-specific site means to match the scale of modeled fluxes most closely. Observed site means were related to the multiple environmental conditions at these sites in a linear regression, weighting sites by the square root of the number of observations (data points) per site. Such relationships likely reflect habitat filtering which commonly leads to trait convergence at community scales. Regressions with the highest explained variance (highest  $R^2_{\text{adjusted}}$ ) were selected, after checking for significance of climatic drivers and distribution of residuals. In case of co-linearity between environmental drivers (Pearson's correlation higher than 0.7 or lower than -0.7), the driver with lowest significance was omitted. Due to the low number of sites for  $V_{\text{max}_{25}}$  and  $J_{\text{max}_{25}}$ , data for the two tropical tree PFTs were combined, as well as data for the two shrub PFTs. This resulted in eight relationships for SLA and six for both  $V_{\text{max}_{25}}$  and  $J_{\text{max}_{25}}$ . These relationships were subsequently implemented in JSBACH. In addition, to allow trait calculations to go beyond climatic regions used in the regressions, but to still maintain traits within ranges as observed in nature, simulated trait ranges were constrained to the 2.5–97.5% quantiles of all individual observations within a PFT (instead of the site means). For  $J_{\text{max}_{25}}$  and  $V_{\text{max}_{25}}$ , an additional constraint was applied to maintain the strong physiological correlation between them (Medlyn et al., 2002; Wullschleger, 1993), keeping  $J_{\text{max}_{25}}$  and  $V_{\text{max}_{25}}$  values within the 95 % confidence interval of the linear regression among

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



these two traits (as determined per PFT). Predicted values outside this range were adjusted to the confidence interval border, based on the shortest distance needed to reach the border. Since this version of JSBACH did not simulate N-cycling, soil N could not be used to parameterize  $V_{\text{cmax}_{25}}$ , even though N-availability is a strong determinant (see references in Kattge et al., 2009). However, the above two constraints on  $V_{\text{cmax}_{25}}$  were based on observational data, indirectly incorporating N-limitations.

## 2.4 Simulation setups

Three different scenarios were performed: 1. a simulation containing the default parameterization of JSBACH with constant parameter values per PFT, based on Raddatz et al. (2007) and Kattge et al. (2009), and adapted to approximate realistic vegetation functioning within the vegetation dynamics module (Brovkin et al., 2009); hereafter called “default simulation”, 2. an “observed traits simulation” again with constant values for SLA,  $V_{\text{cmax}_{25}}$  and  $J_{\text{max}_{25}}$  per PFT, but based on observational data only (the weighted site means for each PFT, from here on called “observed global means”), and 3. a “variable traits simulation” in which traits were allowed to vary depending on local climatic conditions. In the latter simulation, at the beginning of every year each of the three key traits was re-parameterized for each PFT in every terrestrial grid cell of the world, depending on the local simulated climatic conditions in each grid cell. The observed traits simulation was performed in order to separate the effects of replacing trait constants by observations from the effects of trait variation in the model.

To get vegetation into quasi-equilibrium with the simulated climate (but with  $\text{CO}_2$  concentration fixed), the coupled model (JSBACH/ECHAM5) was run for 150 yr with vegetation dynamics in an accelerated mode (i.e. vegetation was simulated 3 times for each year of simulated climate). Next, to get the slow soil carbon pools into equilibrium, the uncoupled carbon model of JSBACH (“CBALANCE”) was run for 1500 yr. The coupled model was continued for 160 yr with updated carbon pools (with the vegetation module in an accelerated mode for the first 50 yr), until carbon pools and vegetation cover had reached equilibrium. The last 10 yr were averaged and used for further analysis,

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



which in this setup (with prescribed seasonal sea surface temperatures) was sufficient to account for the inter-annual climate variation.

## 2.5 Data comparison

Model performance was investigated by comparing vegetation distribution, GPP and biomass of the simulations with observations. Vegetation distribution of the dominant PFT (Fig. 5) was compared to the potential (natural) vegetation map of Ramankutty and Foley (1999), which in part is used to initialize simulations in JSBACH. The mismatch in spatial resolution (the potential vegetation maps is at a global 30 min spatial resolution) was solved by counting the number of PFTs according to Ramankutty and Foley (1999) that were present in each JSBACH-grid cell. The PFT with the highest occurrence was compared with the simulated dominant PFT of JSBACH.

To match the PFT-classifications, aggregated PFTs were constructed (Table S4.1, Fig. S4.1), as the PFTs of Ramankutty and Foley (1999) could not be directly related to those of JSBACH. Temperate and boreal evergreen trees were merged to match extra-tropical evergreen trees in JSBACH. The same was done for deciduous trees. Shrubs (marginal in JSBACH) were merged into a single PFT (“shrubs”) in both JSBACH and the vegetation map. As savannas consist of grasslands and woodlands, matches between savannas and C4-grasses or tropical broadleaved deciduous trees were both classified as correct. Tundra and mixed forests were omitted from the comparison as no equivalent PFT was available in JSBACH.

Model performance was determined with Cohen’s kappa ( $\kappa$ ) (Cohen, 1960), which is the proportion of agreement between vegetation maps, while accounting for chance agreement. Grid cells with sea or ice as the dominant cover were not taken into account, and neither were cases in which more than 1 PFT shared the highest occurrence (i.e. equal number of grid cells). This resulted in a comparison of 2819 grid cells.

Simulated biomass was compared to estimates from Robinson (2007), which include adjusted estimates of belowground (root) carbon in plant biomass. As we simulated only natural vegetation and the estimates of Robinson (2007) are current estimates

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



including land use change and crops, comparing global total biomass would result in an overestimation by our simulations. Therefore, comparisons were made per m<sup>2</sup> per (aggregated) PFT.

JSBACH does not have a separate savanna-like PFT. Therefore, tropical forests and C4-grasslands were averaged and compared with averages of tropical forests and savanna. Furthermore, extra-tropical trees were averaged and compared with averaged temperate and boreal trees of Robinson (2007). Mediterranean shrubs and tundra were omitted as there were no comparable PFTs in JSBACH.

Latitudinal patterns of median GPP were compared with data taken from Beer et al. (2010), who combined observational data (eddy covariance fluxes) with diagnostic models to approximate GPP.

### 3 Results

#### 3.1 Mismatch between observed trait data and default trait settings

Within each PFT, a large observed range in the three trait values was apparent, as well as large overlap in trait ranges among PFTs (Fig. 1). This was most manifest for SLA, where all PFTs overlapped with each other. For Vcmax<sub>25</sub>, the only PFTs of which the 95 % confidence interval did not overlap were both tropical evergreen trees and C4-grasses with C3-grasses and for Jmax<sub>25</sub> both tropical trees and deciduous shrubs with C3-grasses.

For all three traits, the default parameter values deviated strongly from the PFT-specific observed global means (grey diamonds and black circles in Fig. 1) in the observed traits simulation. Differences between these default traits and observed global means of PFTs were on average 32.3 % for Vcmax<sub>25</sub>, 26.8 % for Jmax<sub>25</sub> and 17.3 % for SLA (but for specific PFTs going up to 73.4 %, 57.6 % and 35.2 %, respectively). Kattge et al. (2011) already showed that often PFT-specific constant SLA values in DGVMs differ from the means of observed data, and in some cases even are at the low end of

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the observed data distribution. In JSBACH, SLA default values were always lower than the observed global means, except for the tropical broadleaved deciduous trees, but they almost all fell within the 25 % quartiles of the observed range of SLA, except for deciduous shrubs. However, for both  $V_{max_{25}}$  and  $J_{max_{25}}$  default values fell outside the 25 % quartiles for more than half of the PFTs (five out of eight PFTs for both), and even outside the minimum and maximum values of observed trait ranges in some cases (tropical deciduous trees, C4-grasses and C3-grasses for  $V_{max_{25}}$  and  $J_{max_{25}}$ , and additionally extra-tropical evergreen trees for  $J_{max_{25}}$ ). In contrast to SLA, there was no clear direction of the trait differences for either  $V_{max_{25}}$  or  $J_{max_{25}}$ : half of the default values were lower than the observed global means (Tropical Deciduous Trees, Extra-tropical Evergreen Trees, Raingreen shrubs and C4-grasses), the other half higher. These differences point to a strong mismatch between default trait-parameters in JSBACH with observed natural trait means.

### 3.2 Simulated trait variation based on climatic drivers

The observed variation in PFT-specific site means was related to variation in environmental drivers (Table 2). All regressions were significant, except for C3-grasses for  $V_{max_{25}}$  and for  $J_{max_{25}}$ . Although the selected environmental drivers (Table 2) differed among PFTs, net shortwave radiation (NSWR) and mean annual precipitation (MAP) were most frequently selected as drivers for SLA, as were MAP, mean annual temperature (MAT) and relative humidity (Reh) for  $V_{max_{25}}$  and MAP for  $J_{max_{25}}$ .  $R^2_{adjusted}$  was up to 0.83 for  $V_{max_{25}}$  and 0.71 for  $J_{max_{25}}$ . For SLA, more variation remained unexplained, with a maximum value of 0.40 for  $R^2_{adjusted}$ .

Figure 2 presents the trait ranges of the dominant PFT in every grid cell in the variable traits simulation as predicted by the trait-climate relationships. For each grid cell, only trait values of the dominant PFTs are selected to prevent trait values of marginal PFTs with almost no ecosystem impact to obscure trait ranges most important for model output. Raingreen shrubs were almost never dominant, and predicted variation was low, while deciduous shrubs were never dominant. In contrast to the two runs where

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



PFTs had one constant value per trait, a large climate-driven trait range was predicted for the variable traits simulation. The higher SLA of deciduous versus evergreen trees observed in natural vegetation was reflected in the simulated SLA ranges. As for the observations, there was large overlap in trait ranges among PFTs for the three simulated traits as well, particularly for  $V_{\text{cmax}_{25}}$  and  $J_{\text{max}_{25}}$ . Simulated SLA-ranges were narrower and overlapped less among PFTs compared to observed ranges (Fig. 1). For all three traits, a strong mismatch of default traits with the simulated trait variation was apparent again: for SLA default values fell (at least) outside the 25–75 % inter-quartile range in four PFTs (vs. one in the observed data), and for  $V_{\text{cmax}_{25}}$  and  $J_{\text{max}_{25}}$  for every PFT.

### 3.3 Inclusion of trait variation alters predicted global patterns of productivity

The observed traits and variable traits simulation showed a similar pattern of median GPP along the latitudinal gradient compared to the default simulation (Fig. 3), but in absolute values GPP was much higher in the variable traits simulation in the geographic zone between about 30° S and 30° N (~ 50 % around the equator and twice as much between 25–30° N). GPP of the observed traits simulation also reached higher values (up to twice as much) as the default between 25–30° N, but had lower values than the variable traits simulation between –20° S and 15° N, and highest values (64–67 %) at higher latitudes. NPP differences between about 30° S and 30° N were less profound than for GPP, showing that trait variation affects global patterns of GPP and NPP in different ways. Again, at higher latitudes, the observed traits simulation predicted highest NPP. For the variable traits simulation, the reduction from gross to net primary productivity around the tropics is much stronger than for either other simulation, resulting in smaller NPP differences among simulations compared to GPP differences (even though differences may still go up to 75 % between 25–30° N for both observed and variable traits simulations). The large reduction in differences between NPP and GPP among simulations cannot solely be attributed to a higher respiration of PFTs due to higher  $V_{\text{cmax}_{25}}$  (see Fig. 4), and is mainly a consequence of net productivity

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



exceeding the maximum sizes of the different carbon pools (e.g. of leaves, wood, reserves) as defined in JSBACH, resulting in respiration of excess carbon. This loss of excess carbon is visible in the tropical regions for all simulations, but for the variable traits simulation this resulted in a proportionally larger amount of productivity removed.

This was enhanced by the higher SLA in these regions, which partly determines the amount of carbon stored in the living parts of the plants, consisting of leaves, fine roots and sapwood.

These results show that, while reproducing global patterns of productivity, incorporating global trait variation in the model leads to strong changes in predicted productivity. Even though GPP is not only determined by the photosynthetic parameters ( $V_{cmax_{25}}$  and  $J_{max_{25}}$ ), as it is affected by e.g. water availability as well, on average, shifts in GPP were accompanied by shifts in similar directions by mean  $V_{cmax_{25}}$  and  $J_{max_{25}}$  (weighted by fractional coverage of PFTs), compared to the default simulation (Fig. 4). However, this was not always the case, as e.g. the drop in  $V_{cmax_{25}}$  and  $J_{max_{25}}$  above 40° N did not lead to a coinciding drop in GPP. Productivity could not be related to similar shifts in SLA.

### 3.4 Major shifts in vegetation distribution

Figure 5 and Table 3 show how the global distribution of dominant vegetation types as predicted by the simulations strongly changes when incorporating observed global trait values or including trait variation based on observation-based trait-climate relationships. A PFT was considered dominant if it had the highest fractional coverage in a grid cell; this ranged from coverage of almost 100 % (mostly in tropical regions) to only 30 % in some areas at higher latitudes (see S2 for fractional coverage of the dominant PFTs). Predicted dominant PFTs differed from the default simulation in 35.4 % of the terrestrial grid cells for the variable traits simulation and in 50.5 % of the grid cells for the observed traits simulation.

In the observed traits simulation, tropical evergreen trees, dominant in the default simulation, were taken over by deciduous trees in Africa, South America and Australia

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion









(Fig. 6c, d), but in the variable traits and observed traits simulations it was drier in Canada, Asia and Australia, as well as in large parts of the Amazon rainforests compared to the default simulation.

Compared to the default simulation, in the observed traits simulation mean annual surface-air temperatures were profoundly higher (over 1 °C) in Eastern Siberia, Alaska, the US and Australia, and lower (up to 1 °C) in large parts of Europe and Russia, South-Africa and South-America (Fig. 6a), meaning that (at least) temperature is very sensitive to parameterization of traits.

Temperature differences were less profound between default and the variable traits simulation (Fig. 6b), but still went up to around 1 °C. Changes in temperature did not correlate with clear changes in traits or vegetation shifts (e.g. tree-grass shifts), but in the Southern Hemisphere (Australia, Africa, South-America) corresponded to differences in transpiration, where cooler areas coincided with higher transpiration. This could be related to the higher  $V_{cmax25}$  in these areas, resulting in higher GPP and consequently an increase in transpiration.

The differences between the observed traits simulation and variable traits simulation indicate that by allowing traits to vary and respond to environmental conditions (as in the variable traits simulation) feedbacks between climate and traits result in more moderate temperature shifts, showing the significant magnitude of adaptive traits and on climate.

### 3.6 Comparison of model output with observational data

Cohen's  $\kappa$ , indicating the correspondence of the global map of potential (natural) vegetation of Ramankutty and Foley (1999) with simulated vegetation distribution, was 0.289, 0.282 and 0.334 for the default, observed traits and variable traits simulation, respectively. These values are somewhat lower than the performance of other DGVMs ( $\kappa = 0.42$  for LPJ (Hickler et al., 2006) or  $\kappa = 0.42$  for a consensus map of multiple DGVMs, Cramer et al., 2001). This means that for either simulation, a large proportion of the grid cells did not match the potential vegetation map (Fig. S4.2). However,

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



there is a substantial increase in similarity to observed vegetation from the default and observed traits simulation toward the variable traits simulation.

Mismatches occurred in large parts of the US and Canada, where the simulations predicted mostly C3-grasslands, while according to the potential vegetation map also forests should be present. The same holds for large parts of Europe. The potential vegetation map shows less bare ground than any simulation, resulting in mismatches in the US, but also other parts of the world. Furthermore, almost the whole continent of Australia did not correspond to this map; shrubs and savanna are dominant according to the map, and even though the models did predict C4-grasses there, it was in different areas. Where the default and observed traits simulation had low correspondence with the vegetation map in Africa and South-America, the variable traits simulation performed better, mainly with respect to the tropical trees. Even though differences in performance are small, the variable traits simulation matched the potential vegetation map most closely.

Comparisons of biomass estimates per  $\text{m}^2$  per (aggregated) PFT with current biomass estimates by Robinson (2007), show that for the combined tropical trees and savannas the variable traits simulation ( $13.12 \text{ kg C m}^{-2}$ ) most closely matched biomass estimates ( $12.82 \text{ kg C m}^{-2}$ ) (Table 4). For extra-tropical (temperate and boreal) forest and temperate grasslands, the default simulation underestimates carbon in vegetation, but both the observed traits and variable traits simulation ( $9.64$  and  $9.65 \text{ kg C m}^{-2}$ ) are close to the global estimates for forests ( $10.09 \text{ kg C m}^{-2}$ ). For temperate grasslands, either simulation underestimates biomass, with the default simulation deviation the least from global estimates ( $0.16$  vs.  $0.53 \text{ kg C m}^{-2}$ ), even though differences between simulations are small. Overall, this implies that of the three simulations, the variable traits simulation gives the best global biomass estimates per PFT per  $\text{m}^2$ .

Comparing latitudinal patterns of median GPP with estimates from Beer et al. (2010) (thin blue line in Fig. 3), each simulation produces substantial higher GPP at most latitudes (on average leading to 2, 2.4 and 2.6 times higher GPP for the default, observed traits and variable traits simulation, respectively), with the default simulation in general

## BGD

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



having the smallest differences. However, Chen et al. (2012) suggest that global GPP estimates based on remotely sensed LAI is underestimated by 9 % when leaf clumping is not taken into account, as this would result in an underestimation of the contribution of shaded leaves to GPP, with the strongest underestimation occurring in the tropics.

This implies that the estimates of GPP by Beer et al. (2010) may be too low and thus the actual differences may be less. Also many other DGVMs show higher GPP in the tropical areas than the observed median GPP by Beer et al. (2010) and the GPP estimates of the variable traits simulation still do fall within the upper range of GPP predictions by other DGVMs.

## 4 Discussion

The aim of this study was to improve modeling of vegetation responses and al- low vegetation-atmosphere feedbacks in DGVMs by incorporating trait variation. This trait variation was based on relationships between measured traits and climate and soil moisture, representing major assembly processes by the abiotic environment. As model intercomparisons have shown that large uncertainties exist in projections of land carbon uptake by DGVMs (Cramer et al., 2001; Friedlingstein et al., 2006), incorpo- ration of variation in vegetation responses is important to allow feedbacks between vegetation and climate and to increase plausibility of model predictions, especially un- der strong climate change. Here, we incorporated variation in plant responses based on observed trait and climate data into the JSBACH DGVM, which revealed profound effects on carbon fluxes and vegetation distribution.

### 4.1 Advantages of modeling trait variation based on trait-climate relationships

We used trait-climate relationships to describe the observed natural trait variation and implemented these in JSBACH. The use of such relationships is broadly accepted and applied in ecology (Ordoñez et al., 2010; Wright et al., 2005b) and identifies and

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



captures multiple (approximate) drivers of natural trait variation. The relationships are thought to reflect abiotic assembly processes and integrate multiple vegetation responses at different temporal and spatial scales, including acclimation, adaptation of species and species replacement into a spatially and temporally varying trait mean. Recently, other DGVMs implemented some trait variation necessary to allow feedbacks when modeling N-cycles (Gerber et al., 2010; Zaehle and Friend, 2010). However, in these models effects of trait variation on vegetation cannot be separated from nutrient effects, whereas our study focuses on direct effects of trait variation. Furthermore, the drivers of trait variation in those studies are limited and mainly based on soil N (indirectly included in our study through variation in  $V_{\text{cmax}_{25}}$ ), whereas here multiple drivers of variation have been identified, including water availability (Misson et al., 2006). Even though our proposed method does not explain mechanistically the processes behind trait variation and does not take into account effects of biotic interactions or dispersal on trait values (similar to most DGVMs), it is in our opinion an important and necessary step as it reflects the observed causality between traits and climatic drivers (Niinemets, 2001; St. Paul et al., 2012; Wright et al., 2005b). It has the advantage that it does identify and quantify multiple abiotic drivers of trait means and in this way captures a large part of observed trait variation, as shown by the substantial  $R^2_{\text{adjusted}}$  of most regressions.

We updated trait values once per year. This time-step is a balance between computational efficiency and ecological realism. By this approach we avoid to evaluate ontogenic impacts on trait values and whether environmental impacts differ for different parts of the growing season, for which currently insufficient information is available. Our approach assumes that the yearly updated leaf trait values are in equilibrium with their environments, which is consistent with ecological observations. Compared to e.g. wood traits, the selected leaf traits are rather plastic and can vary within a year (Dubey et al., 2011; Misson et al., 2006). SLA may be somewhat less plastic than the two photosynthetic traits, but a yearly re-parameterization is reasonable, as leaves of deciduous species are shed every year. The maximum lifespan for leaves of evergreen PFTs is

## BGD

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



three years in the model, so shifts occur for at least a third of the leaves for these trees. Moreover, the yearly shift in leaf trait values may not only reflect acclimation, but genetic adaptation and species replacements may also contribute. In our approach, in contrast to a mechanistic approach, the impacts and (unknown) time-scales of those processes leading to trait shifts do not have to be differentiated.

## 4.2 Implications of incorporating observation-based trait variation

The observed global mean trait values of natural vegetation as used in the observed traits simulation strongly deviated from trait values in the default simulation, indicating a mismatch between PFT trait means of modeled and natural vegetation. Moreover, either set of constant values contrasts strongly with the large range of trait values observed in natural vegetation (Fig. 1). While we applied the most comprehensive database available today, we are aware that estimates of observed trait variation are still uncertain (Table 2) and need to be improved in future applications. Nevertheless, the wide range of observed trait values illustrates how simulations with constant traits do not reflect natural trait variation. In contrast, this variation was reflected by the variable traits simulation where trait variation represented abiotic assembly processes (Fig. 2).

To investigate the effects of trait variation on vegetation-climate feedbacks it was essential to incorporate vegetation dynamics, to allow trait shifts to alter vegetation distribution and in this way modulate productivity and climate. In contrast to the simulations with constant traits, the variable traits simulation enabled such interactions between vegetation and climate via traits to occur. These interactions resulted in more spatial variation in dominant vegetation compared to the other two simulations. As such, predicted vegetation distribution is more a result of temporal dynamics in vegetation properties than is the case in the other simulations, where these vegetation properties were prescribed. In such a model setup, direct and indirect effects of traits are not easily disentangled, which makes it difficult to pinpoint how and to what degree traits

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



directly modulated model output. This problem is well known (Quillet et al., 2010) and stresses the importance of simulations like the ones presented.

Provided the strong effect exerted by climate on traits, major differences among the simulations in predicted vegetation distribution and productivity were expected, the latter especially when parameters that affect assimilation rate are concerned, as sensitivity analyses of DGVMs have shown (White et al., 2000; Zaehle et al., 2005). Indeed, for the observed traits simulation and variable traits simulation this resulted in large differences in the new equilibrium state, both compared to the default and to each other. Not only were vegetation properties affected, but also climate changed and mean temperatures were altered by up to more than 1 °C.

As the simulations in this study provide equilibrium states, and as such do not necessarily correspond to current climate or vegetation composition, model comparison to observational data must be interpreted with care, although it does provide insights in the realism of the simulations. DGVMs are parameterized to produce approximately realistic results, and therefore our simulations were not expected to approach observations better than the default simulation. Even though the variable traits simulations produced high GPP for tropical areas, its biomass estimates and vegetation distribution more closely resembled observational data than the default simulation.

The large differences in model output, the mismatch between default trait values in the model and observed trait variation in nature, and the improved performance of the variable traits simulation, demonstrate that – besides a correct representation of plant physiology (e.g. photosynthesis, transpiration) – integration of ecological theory will help to improve vegetation representation in DGVMs and ESMs. Allowing for variable vegetation responses to climate and enabling plant-atmosphere feedbacks will have important consequences for predictions by vegetation models, for vegetation distribution and productivity as well as for global current and future climate. A model intercomparison with this approach under elevated CO<sub>2</sub> projections, for which large uncertainties in predictions by current DGVMs exist (Friedlingstein et al., 2006), should therefore be one of the next steps.

## BGD

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 5 Conclusions

In this study, we have shown how the ecological representation of vegetation responses and vegetation-atmosphere feedbacks in DGVMs can be improved by incorporation of trait variation via trait-climate relationships. The current mismatch of constant trait values in DGVMs with observed natural trait variation and the impact of incorporation of trait variation on model behavior with respect to vegetation distribution, productivity and global climate, together emphasize the need for implementation of more observation-based trait variation and concomitant ecological concepts. The suggested approach, based on such data and concepts, reflects vegetation acclimation and adaptation to the environment, and will enable more reliable modeling of vegetation behavior under unknown climates.

**Supplementary material related to this article is available online at:**  
**<http://www.biogeosciences-discuss.net/9/18907/2012/bgd-9-18907-2012-supplement.pdf>.**

*Acknowledgement.* This study has been financed by the Netherlands Organisation for Scientific Research (NWO), Theme Sustainable Earth Research (project number TKS09-03). Furthermore, this study was supported by the TRY initiative on plant traits (<http://www.try-db.org>). TRY hosted, developed and maintained TRY is hosted, developed and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany) and is supported by DIVERSITAS, IGBP, the Global Land Project, QUEST and GIS “Climat, Environnement et Société” France. The authors are grateful to TERRABITES for stimulation of discussions on modeling traits in the terrestrial biosphere. Finally, the authors thank Veronika Gayler (Max Planck Institute for Meteorology, Hamburg, Germany) for the technical and methodological support on JSBACH/ECHAM5.

**BGD**

9, 18907–18950, 2012

### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





## References

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### Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





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**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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- 30

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thebault, A., Vile, D., and Zarovali, M. P.: Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites, *Ann. Bot-London.*, 99, 967–985, doi:10.1093/aob/mcm215, 2007.

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**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





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## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Table 1.** References for trait data used in this study.

Reference	SLA	Vcmax <sub>25</sub>	Jmax <sub>25</sub>
Ackerly and Cornwell (2007)	x		
Bahn et al. (1999)	x		
Cavender-Bares et al. (2006)	x		
Cornelissen et al. (2003)	x		
Cornelissen et al. (2004)	x		
Cornwell et al. (2006)	x		
Domingues et al. (2010)		x	x
Fyllas et al. (2009)	x		
Garnier et al. (2007)	x		
Kattge et al. (2009)	x	x	x
Kattge et al. (2011)	x		
Kleyer et al. (2008)	x		
Kurokawa and Nakashizuka (2008)	x		
Kurokawa (2012)	x		
Laughlin et al. (2010)	x		
Leishman (2012)	x		
Louault et al. (2005)	x		
Medlyn et al. (1999)	x		
Niinemets (1999)	x	x	
Niinemets (2001)	x	x	
Ogaya and Penuelas (2007)	x		
Ogaya and Penuelas (2008)	x		
Ordoñez et al. (2010)	x		
Patino et al. (2012)	x		
Pyankov et al. (1999)	x		
Reich et al. (2008)	x		
Reich et al. (2009)	x		
Shipley (1995)	x		
Shipley and Vu (2002)	x		
Soudzilovskaia (2012)	x		
Swaine (2007)	x		
van Bodegom et al. (2012)	x		
van Bodegom (2012)	x		
Vile et al. (2006)	x		
Weiherr (2012)	x		
Wohlfahrt et al. (1999)	x		
Wright et al. (2004)	x		
Wright et al. (2006)	x		

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Table 2.** Properties of the selected trait-climate relationships used to re-parameterize traits.

	Nr of sites <sup>1</sup> (observations)	Environmental drivers of traits <sup>2</sup>	$R^2_{\text{adjusted}}$ of relation- ships	Lower and upper boundaries <sup>3</sup>
SLA ( $\text{m}^2 \text{kg}^{-1}$ carbon)				
Tropical evergreen trees	69 (933)	-MAP,-NSWR, (+int)	0.092	7.41, 48.29
Tropical deciduous trees	38 (129)	-Tmin,-MAP,+Reh	0.30	12.07, 49.54
Extra-tropical evergreen trees <sup>4</sup>	363 (308)	+MAT,+MAP,-NSWR	0.29	4.58, 42.46
Extra-tropical deciduous trees <sup>4</sup>	177 (282)	-Tmax,-Reh,(+int)	0.056	6.24, 90.50
Raingreen shrubs	178 (696)	-MAP,-NSWR	0.26	3.66, 72.69
Cold/Deciduous shrubs	39 (111)	+MAT	0.13	17.82, 61.53
C3-grasses	153 (309)	+Tmax, +Reh	0.12	3.08, 96.58
C4-grasses	35 (101)	-NSWR	0.40	5.41, 72.19
Vcmax <sub>25</sub> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )				
Tropical evergreen trees & Tropical deciduous trees <sup>5</sup>	9 (85)	+MAT,+MAP, (-int)	0.83	18.0, 67.7
Extra-tropical evergreen trees	15 (284)	+MAT,-MAP,+Reh	0.28	18.4, 179.9
Extra-tropical deciduous trees	19 (273)	-Reh,-SoilMoist, (+int)	0.34	18.2, 130.0
Raingreen shrubs & Cold/Deciduous shrubs <sup>5</sup>	15 (75)	-MAP,-Reh, (+int)	0.45	25.1, 129.1
C3-grasses	4 (15)	-MAT	0.37	24.4, 118.4
C4-grasses	8 (29)	+NSWR	0.51	21.7, 46.3
Jmax <sub>25</sub> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) – for C4-grasses: PEP ( $\text{mmol m}^{-2} \text{s}^{-1}$ )				
Tropical evergreen trees & Tropical deciduous trees <sup>5</sup>	9 (51)	+MAT,+MAP, (-int)	0.68	35.8, 121.6
Extra-tropical evergreen trees	12 (113)	+Tmin,-MAP	0.28	57.5, 329.6
Extra-tropical deciduous trees <sup>6</sup>	10 (135)	+Tmin,+NSWR, (-int)/ -MAP,- SoilMoist, (+int)	0.71 / 0.44	41.1, 206.9
Raingreen shrubs & Cold/Deciduous shrubs <sup>5</sup>	13 (59)	+MAP, -SoilMoist	0.64	65.4, 223.5
C3-grasses	4 (15)	-MAT	0.63	42.8, 230.6
C4-grasses	8 (29)	+NSWR	0.51	92.3, 465.4

<sup>1</sup>: Number of sites available for the regression analysis, in brackets the number of observations of these sites.

<sup>2</sup>: Environmental drivers are mean annual temperature (MAT), mean temperature of coldest and warmest month (Tmin and Tmax), mean annual precipitation (MAP), mean annual relative humidity (Reh), soil moisture (SoilMoist) and net shortwave radiation (NSWR). + = positive relationship, – = negative relationship, (int) = interaction effect between two drivers.

<sup>3</sup>: Lower and upper boundaries of the predicted traits in the variable traits simulation, based on the 2.5 and 97.5 quantiles of all individual observations within PFTs.

<sup>4</sup>: Extra-tropical trees include both temperate and boreal trees.

<sup>5</sup>: For Vcmax<sub>25</sub> and Jmax<sub>25</sub>, tropical trees have the same relationships with climatic drivers, as they were combined due to low number of sites. The same holds for shrubs.

<sup>6</sup>: As the best model covered a relatively small climatic range, an additional regression model was applied to these areas that fell outside the climatic range of the first model.

**BGD**

9, 18907–18950, 2012

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



# Trait variation in an ESM

L. M. Verheijen et al.

**Table 3.** Dominant PFT coverage (%) of vegetated grid cells for the three different simulations.

PFT	Default simulation	Observed traits simulation	Variable traits simulation
Tropical evergreen trees	23.06	0	12.55
Tropical deciduous trees	0.024	21.38	7.89
Extra-tropical evergreen trees	13.64	36.31	21.45
Extra-tropical deciduous trees	14.72	0	8.66
Raingreen shrubs	3.66	1.30	0.12
Cold/Deciduous shrubs	0.048	0	0
C3-grasses	24.58	24.50	21.47
C4-grasses	4.83	5.19	8.37
Bare surface	15.44	11.32	19.50

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[I◀](#)
[▶I](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


# Trait variation in an ESM

L. M. Verheijen et al.

**Table 4.** Biomass estimates from Robinson (2007) compared to simulated biomass of the three simulations.

Robinson PFT	Biomass (kg C m <sup>-2</sup> )	JSBACH PFT	Biomass (kg C m <sup>-2</sup> )		
			Default simulation	Observed traits simulation	Variable traits simulation
Tropical forest	22.23	Tropical evergreen forest	16.15	14.63	22.07
Savannah & grassland	3.41	Tropical deciduous forest	10.84	17.55	16.96
		C4-grasses	0.31	0.29	0.32
<b>Average:</b>	<b>12.82</b>		<b>9.10</b>	<b>10.82</b>	<b>13.12</b>
Temperate forest	15.29	Extra-tropical evergreen forest	5.79	10.96	9.04
Boreal forest	4.89	Extra-tropical deciduous forest	8.38	8.33	10.25
<b>Average:</b>	<b>10.09</b>		<b>7.08</b>	<b>9.64</b>	<b>9.65</b>
Temperate grassland	0.53	C3-grasses	0.16	0.13	0.12

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

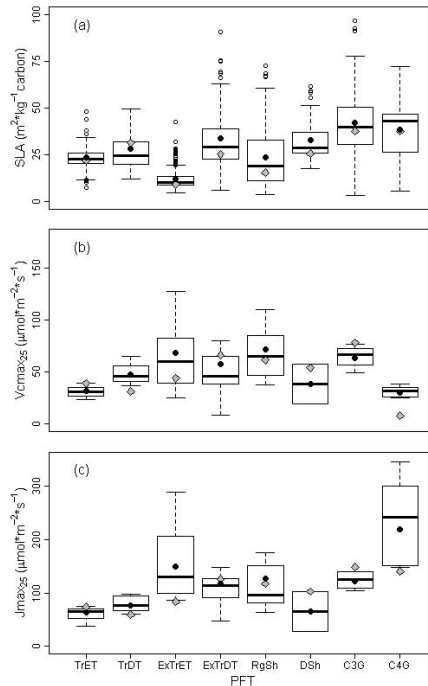
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Full Screen / Esc

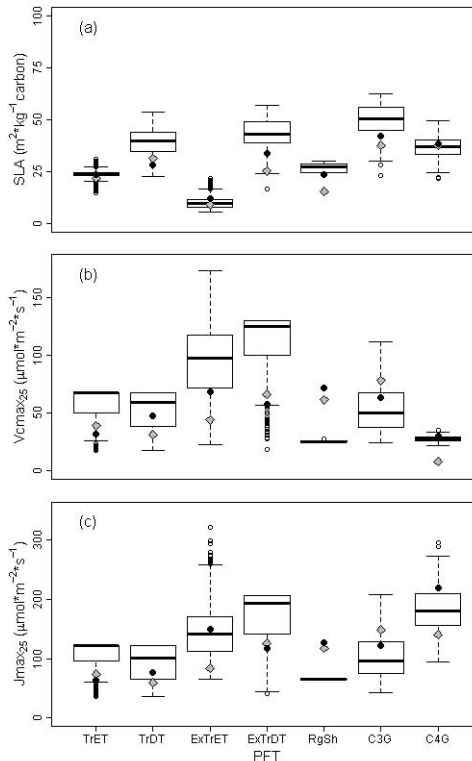
Printer-friendly Version

Interactive Discussion



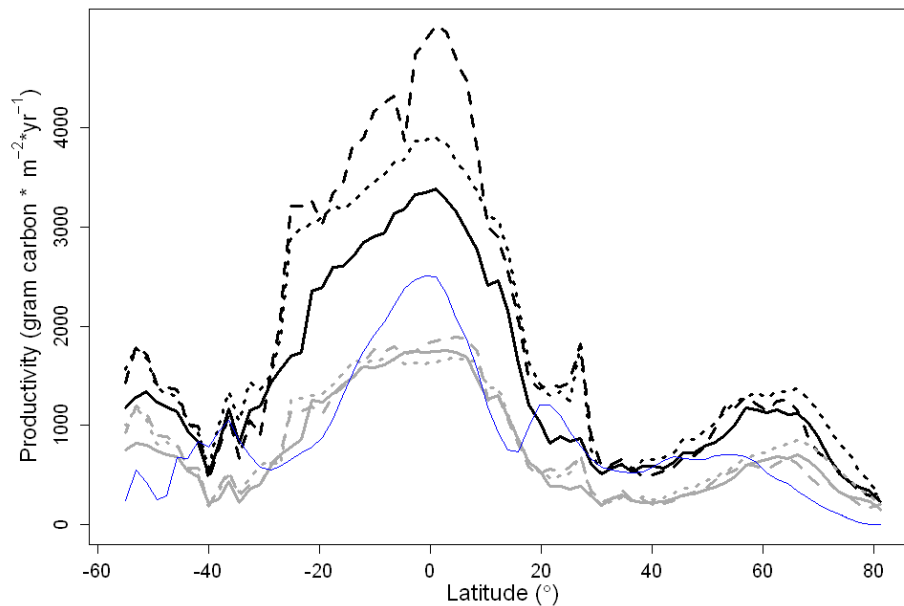


**Fig. 1.** Observed trait ranges of PFT-specific site means: **(a)** SLA ( $\text{m}^2 \text{kg}^{-1} \text{carbon}$ ), **(b)**  $V_{\text{cmax}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), **(c)**  $J_{\text{max}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). For C4-grasses, PEPcase  $\text{CO}_2$ -specificity (PEP) in  $\text{mmol m}^{-2} \text{s}^{-1}$  is modeled. Boxplots show the median (middle line), the 25 % and 75 % quartiles (hinges), the outer value within the  $1.5 \times \text{interquartile range}$  (whiskers) and outliers (open circles). Grey diamonds are trait values used in the default simulation, black circles are observed global means used in the observed traits simulation and therefore don't match the medians in the boxplots. PFTs are tropical broadleaved evergreen trees (TrET), tropical broadleaved deciduous trees (TrDT), extra-tropical (both temperate and boreal) evergreen trees (ExTrET), extra-tropical deciduous trees (ExTrDT), raingreen shrubs (RgSh), cold/deciduous shrubs (DSh), C3-grasses (C3G) and C4-grasses (C4G).

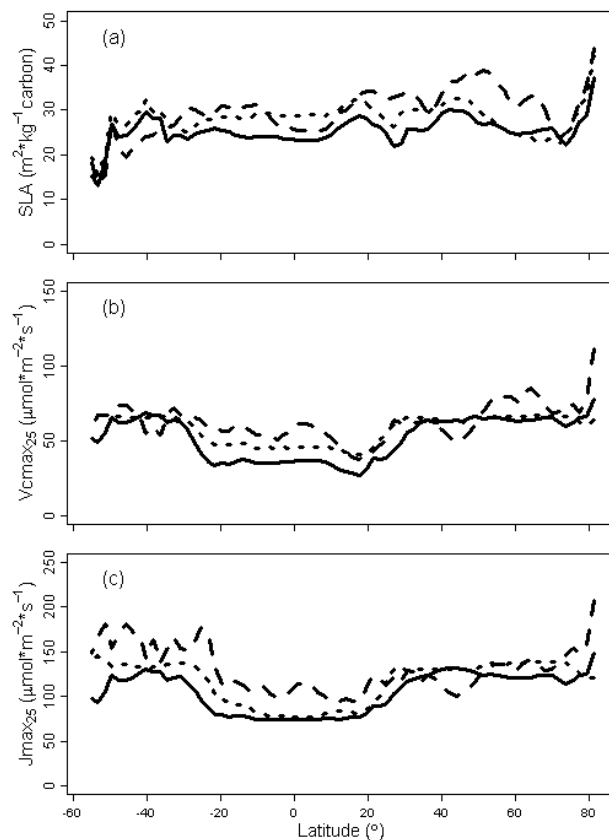


**Fig. 2.** Simulated trait ranges of the dominant PFTs of each grid cell in the variable traits simulation: **(a)** SLA ( $\text{m}^2 \text{kg}^{-1} \text{carbon}$ ), **(b)**  $V_{\text{cmax}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), **(c)**  $J_{\text{max}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). For C4-grasses, PEPcase  $\text{CO}_2$ -specificity (PEP, in  $\text{mmol m}^{-2} \text{s}^{-1}$ ) instead of  $J_{\text{max}_{25}}$  is modeled. Boxplots and symbols as in Fig. 1. PFTs as in Fig. 1 but without cold/deciduous shrubs (DSh), because this PFT was never dominant. Observed global means are added again for illustrative purposes. Note that direct comparison with simulated data is not appropriate here as the range of climatic conditions do not overlap for observed and simulated trait data.

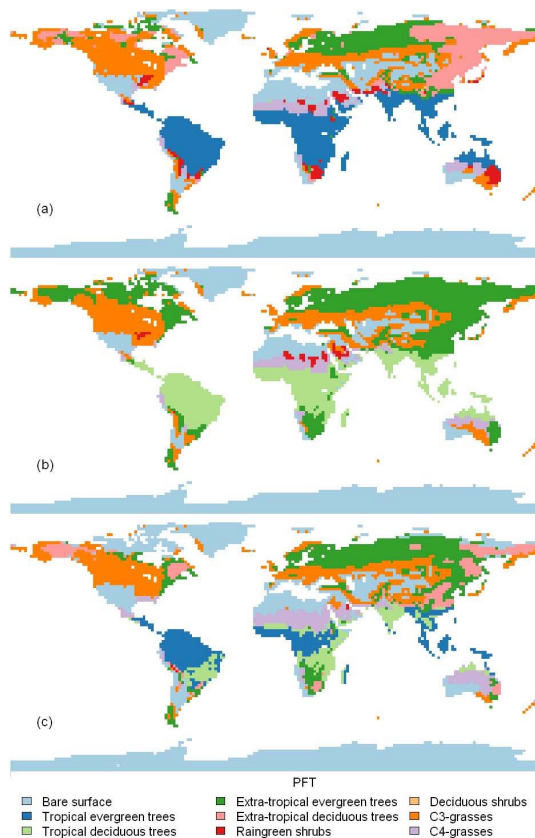




**Fig. 3.** Latitudinal gradient of median GPP and NPP. Continuous line default simulation, dotted line observed traits simulation, dashed line variable traits simulation. Black lines GPP, grey lines NPP. Thin blue line median GPP taken from Beer et al. (2010).



**Fig. 4.** Latitudinal gradient of mean trait values weighted by fractional cover of the PFTs. **(a)** SLA ( $\text{m}^2 \text{kg}^{-1} \text{carbon}$ ), **(b)**  $V_{\text{cmax}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), **(c)**  $J_{\text{max}_{25}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). For  $J_{\text{max}_{25}}$ , C4-grasses are left out as PEP instead of  $J_{\text{max}_{25}}$  is modeled for this PFT. Continuous line default simulation, dotted line observed traits simulation, dashed line variable traits simulation.



**Fig. 5.** Global distribution of dominant PFTs. **(a)** Default simulation, **(b)** observed traits simulation and **(c)** variable traits simulation.

## Trait variation in an ESM

L. M. Verheijen et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

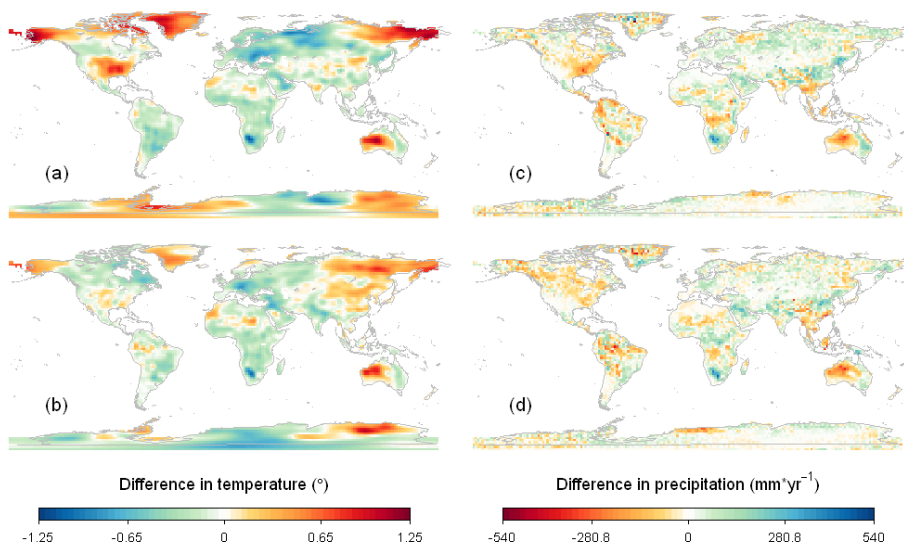
Printer-friendly Version

Interactive Discussion



## Trait variation in an ESM

L. M. Verheijen et al.



**Fig. 6.** Difference in mean annual temperature and annual precipitation. Observed traits simulation minus default simulation **(a)** for temperature and **(c)** precipitation, and variable traits simulation minus default simulation for **(b)** for temperature and **(d)** precipitation.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[I◀](#)
[▶I](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)
