Sensitivity analysis of a process-based ecosystem model: Pinpointing parameterization and structural issues

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[1]   Dynamic vegetation models have been widely used for analyzing ecosystem dynamics and their interactions with climate. Their performance has been tested extensively against observations and by model intercomparison studies. In the present analysis, Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS), a state-of-the-art ecosystem model, was evaluated by performing a global sensitivity analysis. The study aims at examining potential model limitations, particularly with regard to long-term applications. A detailed sensitivity analysis based on variance decomposition is presented to investigate structural model assumptions and to highlight processes and parameters that cause the highest variability in the output. First- and total-order sensitivity indices were calculated for selected parameters using Sobol's methodology. In order to elucidate the role of climate on model sensitivity, different climate forcings were used based on observations from Switzerland. The results clearly indicate a very high sensitivity of LPJ-GUESS to photosynthetic parameters. Intrinsic quantum efficiency alone is able to explain about 60% of the variability in vegetation carbon fluxes and pools for a wide range of climate forcings. Processes related to light harvesting were also found to be important together with parameters affecting forest structure (growth, establishment, and mortality). The model shows minor sensitivity to hydrological and soil texture parameters, questioning its skills in representing spatial vegetation heterogeneity at regional or watershed scales. In the light of these results, we discuss the deficiencies of LPJ-GUESS and possibly that of other, structurally similar, dynamic vegetation models and we highlight potential directions for further model improvements.

1.   Introduction

[2]   Understanding and simulating the terrestrial carbon cycle continue to be great challenges [*Pitman et al.*, 1990; *Bonan et al.*, 1992; *Cox et al.*, 2000; *Cramer et al.*, 2001; *Melillo et al.*, 2002; *Moorcroft*, 2006; *Heimann and Reichstein*, 2008; *Purves and Pacala*, 2008]. The role of vegetation is of paramount importance since it regulates the transport of water, carbon, energy, and momentum at the land surface, via many nonlinear biophysical and biochemical processes [*Pitman*, 2003; *Bonan*, 2008b; *Heimann and Reichstein*, 2008; *Arneth et al.*, 2010; *Anderson et al.*, 2011; *Fatichi et al.*, 2012a]. Many numerical models, reflecting different degrees of complexity and abstraction, were developed mimicking terrestrial ecosystem structure and dynamics. The need for a better understanding and representation of the biosphere, as well as an increasing interest in investigating the terrestrial carbon cycle, contributed to the development of process-based terrestrial ecosystem models [*Foley*, 1994; *Liu et al.*, 1997; *Purves and Pacala*, 2008; *Levis*, 2010; *McMahon et al.*, 2011]. Process-based models are very often used as reliable tools for investigating the effect of climate and anthropogenic intervention on short- and long-term vegetation dynamics [*Melillo et al.*, 1993; *Cox et al.*, 2000; *Moorcroft*, 2003; *Evans*, 2012]. In the present study, we are focusing on Dynamic Global Vegetation Models (DGVMs) [*Peng*, 2000; *Ostle et al.*, 2009; *Levis*, 2010; *Quillet et al.*, 2010]. Dynamic Global Vegetation Models (DGVMs) have been extensively used for simulating the terrestrial carbon balance and for assessing changes and feedbacks in vegetation structure and productivity due to climate variability [e.g., *Cramer et al.*, 2001; *Bachelet et al.*, 2003; *Morales et al.*, 2007; *Zaehle et al.*, 2007; *Le Quéré et al.*, 2009].

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[3] Testing model performance against observations and model intercomparisons are important steps for model evaluation [Hurtt et al., 1998; Moorcroft, 2006; Quillet et al., 2010]. Although absolute verification and validation of numerical models are basically impossible as natural systems are never closed [Oreskes et al., 1994], model confirmation in relative terms can be obtained by comparing model output with observed variables. The recent increase in data quantity and quality especially due to eddy-flux tower networks [Baldocchi et al., 2001; Baldocchi, 2008], remote sensing products [Myneni et al., 2002; Kerr and Ostrovsky, 2003], and forest inventories [Frayer and Furnival, 1999; Lischke and Löffler, 2006] offers a great chance for assessing model performance against multiple variables and data sets. The use of these data sets led to numerous model applications assessing the skill of terrestrial biosphere models in reproducing current ecosystem variables [e.g., Kucharik et al., 2000; Cramer et al., 2001; Bachelet et al., 2003; Hickler et al., 2004; Krinner et al., 2005; Kucharik et al., 2006; Beer et al., 2010; Medvigy and Moorcroft, 2012]. There are also many intercomparison studies among different terrestrial ecosystem models, testing the consensus of a variety of model structures and parameterizations [Cramer et al., 1999, 2001; House et al., 2003; Morales et al., 2005; Friedlingstein et al., 2006; Ito and Sasai, 2006; Luo et al., 2008; Sitch et al., 2008; Schwalm et al., 2010; Dietze et al., 2011; Haddeland et al., 2011; Wang et al., 2011; Wolf et al., 2011; Keenan et al., 2012].

[4] While many intercomparison studies showed substantial differences among the results of process-based models, few mechanistic explanations on the reasons of their poor agreement are usually provided [Cramer et al., 1999; Roxburgh et al., 2004; Ito and Sasai, 2006; Jung et al., 2007b, a]. Discrepancies among DGVMs raise doubts about their robustness and reliability [Morales et al., 2005], illustrating that a predictive modeling framework of the biosphere is still problematic [Moorcroft, 2006; Heimann and Reichstein, 2008; Fisher et al., 2010; Richardson et al., 2011; Evans et al., 2012]. Therefore, a better process representation and a more accurate parameterization of terrestrial ecosystem models are required.

[5] Model development and improvements of their performance based only on model intercomparison studies or model evaluation against observations can be difficult due to the high complexity and dimensionality of model structures. In fact, intrinsic structural model uncertainties can often be compensated through parameter adjustments [Chen et al., 2011; Bonan et al., 2011], leading to satisfactory model performance and realistic results, without providing a holistic understanding of the system [Medlyn et al., 2005; Beven, 2006; Keenan et al., 2011a]. In addition, while model evaluation against observed variables and model intercomparison studies are fundamental for describing the overall structural model uncertainty and discrepancies, they provide only partial information about the sources of bias and uncertainties, especially when metrics summarizing many processes are used in the comparison.

[6] Sensitivity analysis, i.e., the study of how the uncertainty in model realizations is apportioned to different sources of uncertainty in the model inputs, is considered one of the major steps for model evaluation as well as a very elegant test highlighting model limitations and directions of further improvements [Sheng et al., 1993; Saltelli and Scott, 1997; Saltelli et al., 2000b; Medlyn et al., 2005; Jakeman et al., 2006; Cariboni et al., 2007]. The need for well-designed, rigorous global sensitivity analysis (GSA) is reinforced due to (1) the intrinsic complexity of terrestrial ecosystems that is typically translated in the DGVMs' framework through nonlinear relationships among processes (e.g., photosynthesis, respiration, and stomatal regulation) and environmental variables (e.g., air temperature, radiation, and CO_2 concentration) [Jarvis, 1995; Baldocchi et al., 2002; Cox et al., 2006; Kimmins et al., 2008], (2) the large number of parameters (i.e., many degrees of freedom) that this type of models includes [Manson, 2001; Lawrie and Hearne, 2007; Tang and Bartlein, 2008], (3) the physically based framework of DGVMs, implying that the sensitivity of the implemented components should also reflect the sensitivity of the real processes. Therefore, sensitivity analysis can be seen as an important step for model evaluation. Advanced statistical techniques are strongly recommended for performing a thorough GSA, not only accounting for first-order parameter effects but also assessing the effect of interactions among different parameters and processes [Saltelli et al., 2000, 2004, 2008].

[7] Surprisingly, the variety of terrestrial ecosystem models, their increasing degree of sophistication, and their numerous applications are usually followed by a scarcity of proper sensitivity analyses, ignoring European [EC, 2009] and American [EPA, 2009] guidelines about best modeling practices. Despite the vast amount of GSA methodologies and literature covering this topic [e.g., Hamby, 1994; Saltelli et al., 2000; Frey and Patil, 2002; Saltelli et al., 2004; Cariboni et al., 2007; Saltelli et al., 2008, 2006], practitioners and modelers very often choose simplistic approaches for investigating parameter uncertainty and sensitivity, which are prone to numerous problems [Saltelli, 1999; Saltelli and Annoni, 2010].

[8] Taking into account that sensitivity analysis is an essential step for model development, improvement, and evaluation, we performed a detailed GSA, based on a state-of-the-art methodology, for a well-established DGVM: the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) [Smith et al., 2001; Sitch et al., 2003; Gerten et al., 2004]. Many studies have been published demonstrating the skill of LPJ and LPJ-GUESS in predicting potential vegetation and productivity at global and regional scales [e.g., Morales et al., 2005; Hély et al., 2006; Koca et al., 2006; Morales et al., 2007; Hickler et al., 2012]. The uncertainty in LPJ and LPJ-GUESS results was also assessed by Zaehle et al. [2005] and Wramneby et al. [2008] respectively.

[9] The present study conducts for the first time a variance-based GSA of a representative DGVM. Parameters covering the entire spectrum of simulated processes are included in the analysis. In order to elucidate the role of climate on model sensitivity, different climatic forcings, based on meteorological data from Switzerland, are selected. This study not only allows for identification of the most influential parameters (which is the typical objective of many published sensitivity analyses) but also goes a step further. Specifically, the following questions are posed: (1) does the sensitivity (or the lack of sensitivity) of the implemented components reflect the sensitivity of the real

processes? (2) Is there any dominant process (characterized by a group of parameters) that controls model response?

[10] On the basis of the GSA analysis, structural and conceptual deficiencies underlying LPJ-GUESS are therefore highlighted and suggestions for potential improvements of DGVMs are discussed. While differences may exist in the way specific components are parameterized in different DGVMs (e.g., photosynthesis, transpiration, and soil biogeochemistry), the general model structure and the environmental controls are mostly similar [*Levis*, 2010; *Quillet et al.*, 2010]. Therefore, we argue that our conclusions are not limited to the LPJ family of models but are relevant for many other terrestrial ecosystem models.

2. Methodology

2.1. The Lund-Potsdam-Jena General Ecosystem Simulator

[11] LPJ-GUESS is a state-of-the-art terrestrial biogeochemical model of forest growth which combines LPJ-DGVM [*Sitch et al.*, 2003] with a more detailed representation of vegetation dynamics, GUESS [*Smith et al.*, 2001]. A short overview of the features and assumptions of LPJ-GUESS is provided here. A more detailed model description can be found elsewhere [*Smith et al.*, 2001; *Sitch et al.*, 2003; *Gerten et al.*, 2004], as well as numerous model applications in different locations worldwide [*Badeck et al.*, 2001; *Hickler et al.*, 2004; *Morales et al.*, 2005; *Hély et al.*, 2006; *Koca et al.*, 2006; *Morales et al.*, 2007; *Wolf et al.*, 2008; *Hickler et al.*, 2012].

[12] LPJ-GUESS has a process-based representation of land-atmosphere carbon and water exchange and embeds a mechanistic approach for mimicking terrestrial vegetation dynamics. Key ecosystem processes such as photosynthesis, respiration, stomatal regulation, plant phenology, and soil biogeochemistry as well as soil hydrological processes are simulated daily. Processes related to forest successional dynamics such as plant growth, establishment, and mortality are computed annually. Vegetation properties are assigned using plant functional types (PFTs), a classification that groups plants based on their major functional traits [*Bonan et al.*, 2002]. Each PFT has predefined physiological and bioclimatic attributes (Table 1) which determine whether the prevailing climate conditions are favorable or not for its establishment and growth, i.e., different PFTs occur in different climates. The model version used in this study includes the hydrological improvements presented by *Gerten et al.* [2004]. While LPJ

and LPJ-GUESS apply identical modules for simulating land-atmosphere coupling and plant-level carbon dynamics, their main difference, which optimizes LPJ-GUESS for regional applications, lies in the representation of vegetation dynamics [*Smith et al.*, 2001]. LPJ-GUESS, similarly to other individual-based models [e.g., *Moorcroft et al.*, 2001; *Sato et al.*, 2007; *Medvigy et al.*, 2009], uses a mechanistic approach based on forest gap models (e.g., *Prentice et al.* [1993]), for mimicking vegetation heterogeneity at the local scale. Forest structure is represented by simulating 100 replicated patches of potential PFTs with different age classes (cohorts). The use of several replicated patches accommodates for the variability due to stochastic processes such as plant establishment and mortality. In the present study, three PFTs were used: two woody PFTs (needle-leaved evergreen, NE, and broad-leaved summergreen, TBS) and one generic herbaceous (C_3 grass, GRS). The parameterization of PFTs is based on previous works of *Hickler et al.* [2004], *Miller et al.* [2008], and *Sitch et al.* [2003]. Fire disturbances were not used in the current study. Only a generic background mortality represented by stochastic disturbances (e.g., storms and diseases) was considered for the sensitivity analysis experiment. Simulation starts with no vegetation (i.e., bare ground); therefore for each parameter set, a period of 1000 years (constructed by repeating randomly years of the observed climate), with preindustrial CO_2 levels, was used to spin up the model and define the initial states of carbon pools and vegetation cover in equilibrium with the climate forcing (spin-up simulation period). Starting from the steady state obtained after the spin-up, the model was successively driven with daily data (section 2.2) based on the historical Swiss meteorological records (historical simulation period). The sensitivity analysis was carried out only for the historical simulation period.

2.2. Climate Data

[13] LPJ-GUESS uses meteorological measurements of daily precipitation, temperature and sunshine hours, and annual values of CO_2 concentration as climate forcings. Atmospheric CO_2 concentrations were derived from ice core reconstructions [*Sitch et al.*, 2003; *Frank et al.*, 2010] and the Mauna Loa record [*Keeling et al.*, 2009]. We carried out plot-scale simulations for which no explicit spatial dimension is required. In order to investigate the model sensitivity under different climate conditions, virtual stations, representative of the entire Switzerland, were generated, covering a wet to dry gradient and a wide range of elevations. Daily climate forcings were defined following a detailed analysis of 200 Swiss meteorological stations with high-quality measurements of precipitation, temperature, and radiation (Figure 1). Three stations were identified as representative for dry, normal, and wet conditions with about 600 (Sion), 1300 (Chaumont), and 2000 (Ebnat-Kappel) mm/year of annual precipitation. Observed precipitation and radiation time series from these stations, from 1 January 1966 to 30 December 2009 (44 years), were used in the analysis (Table 2). Temperature time series measured at the meteorological station of Chaumont, 1073 m asl, was used to force the model, after applying an environmental temperature lapse rate of, i.e., 6.5°C/km. This operation allows us to generate five virtual elevation bands (i.e., different temperature time series) from 200 to 2600 m asl with a 600 m interval (Table 2), covering the entire range of

Table 1. Plant Functional Types (PFTs) Used for the Analysis, Abbreviations, and Bioclimatic Limits

	NE	TBS	GRS
PFT	Shade-tolerant needle-leaved evergreen	Shade-tolerant broad-leaved summergreen	Grass
Photosynthesis pathway	C_3	C_3	C_3
GDDmin[a]	600	1500	—
Tc, min[b]	−30	−3.5	—
Tc, max[c]	−1.5	6	—

[a]Minimum degree-days sum (5°C base) for establishment (°C).
[b]Minimum coldest month temperature for survival (°C).
[c]Maximum coldest month temperature for establishment (°C).

vegetated area in Switzerland. The climate types used for the GSA are therefore a combination of the three identified precipitation-cloud cover patterns (dry, normal, and wet) with five different temperature time series representative of different elevation bands (15 virtual stations in total). Although the synthetic climate forcings (virtual stations) were based only on Swiss records, they are likely to be representative of much larger area due to the wide range of precipitation and temperature regimes covered by the analysis (Table 2).

2.3. Sensitivity Analysis

[14] A detailed description of the methodology applied for the GSA is provided in the supporting information, and just the outlines are summarized in the following sections.

[15] The structure of LPJ-GUESS is complex, including many simulated processes and potentially many interactions; therefore, no a priori assumption can be made about the linearity, monotonicity, or additivity of the model response to parameter changes. In these conditions, commonly applied practices of simply changing one-parameter-at-a-time are considered inappropriate [*Saltelli and Annoni*, 2010]. In the present analysis, LPJ-GUESS is treated as black-box, without assumptions about its structure (i.e., model-free approach). Furthermore, since model outputs are time series, the mean of each output variable over the 44 years of the historical period (i.e., starting from the spun-up conditions) is used for the sensitivity analysis. This allows us to assess the model sensitivity, filtering the influence of variability induced by interannual or seasonal climate and vegetation fluctuations. The methodology used for the GSA of LPJ-GUESS is summarized in four steps:

[16] 1. Selection of the output of interest. Since LPJ-GUESS has many different output variables (vegetation and soil carbon as well as water fluxes and states), the model sensitivity is expected to be different according to the selected model output. In the present study, we focused on the following variables: net primary productivity, NPP ($NPP = GPP - R$, where GPP denotes the gross primary production and R is the sum of plant maintenance and growth respiration) and vegetation carbon pools (i.e., the sum of leaves, sapwood, heartwood, and fine roots, carbon).

[17] 2. Selection of parameter ranges and distributions. Key parameters for the principal processes were identified and included in the analysis (section 2.3.1).

[18] 3. Qualitative GSA. A screening test was applied to identify a subset of the most important parameters. The purpose of the screening sensitivity analysis is to gain insights into the importance of parameters with low computational cost (section 2.3.2).

[19] 4. Quantitative GSA. An explicit, quantitative evaluation of parameter importance and interactions was performed for the subset of parameters identified in the screening sensitivity analysis. A variance-based GSA technique is used for this task (section 2.3.3).

### 2.3.1. Parameter Ranges and Assumptions

[20] On the basis of extensive literature research and model structure investigation, 34 model parameters, which are linked to the main simulated processes, namely, parameters related to plant establishment, growth, and mortality, soil organic matter dynamics, plant biochemical and biophysical processes, plant-water demand and uptake, and hydrological processes (e.g., runoff and percolation), were selected for the GSA. The model sensitivity to soil texture and soil characteristics was also investigated by including in the GSA the parameter regulating the soil water storage capacity available to plants, SSC (Table 3).

[21] Parameter ranges represent a very critical but unavoidable choice for any sensitivity analysis study [*Wallach and Genard*, 1998]; therefore, a thorough selection has to be made. According to suggested guidelines [*Wallach and Genard*, 1998], GSA requires a detailed coverage of the entire parameter space over the full range of plausible values. Particular attention is thus paid in defining the uncertainty ranges of the examined parameters (see Table 3, and references therein). More specifically, for well-documented parameters, the range obtained from measurement variability was used, while for empirical parameters, a plausible range was approximated based on our current knowledge, modeling experience, and literature survey (Table 3).

[22] Model parameters are treated as independent random variables and their uncertainty is characterized by a uniform Probability Density Function (PDF). Parameter independence is a crude but necessary assumption since our current knowledge about ecosystem processes does not allow for quantitatively predefined correlations. The orthogonality of the parameter space also facilitates the sensitivity analysis since it enhances applicability and computations of many GSA methodologies. The choice of a noninformative PDF, such as the uniform, reflects the lack of knowledge which does not allow us to assign a well-defined distribution (see also *Radtke et al.* [2001]; *Medlyn et al.* [2005]). It is also coherent with other studies that mostly used uniform PDFs [e.g., *Zaehle et al.*, 2005; *Wramneby et al.*, 2008]. These conservative assumptions may lead to overestimation of model uncertainty and sensitivity since improbable parameter combinations can be included. In order to partially reduce this effect and preserve the trait differences among plant types, PFT specific parameters were adjusted in their uncertainty range by maintaining a constant ratio between the different PFTs, derived from the standard model parameterization.

Table 2. Climatic Forcings Used for the Sensitivity Analysis Based on Observations From 200 Swiss Meteorological Stations. The Temperature-based Elevation Bands are Created According to the Meteorological Station of Chaumont

	Mean Precipitation (mm)			Mean temperature (°C)				
	Dry	Normal	Wet	200 m	800 m	1400 m	2000 m	2600 m
Annual	600	1245	1898	11.8	7.9	4.0	0.1	−3.8
Winter	163	315	414	4.4	0.5	−3.4	−7.3	−11.2
Spring	123	288	457	10.6	6.7	2.8	−1.1	−5.0
Summer	166	336	604	19.4	15.5	11.6	7.7	3.8
Autumn	148	305	424	12.4	8.5	4.6	0.7	−3.2
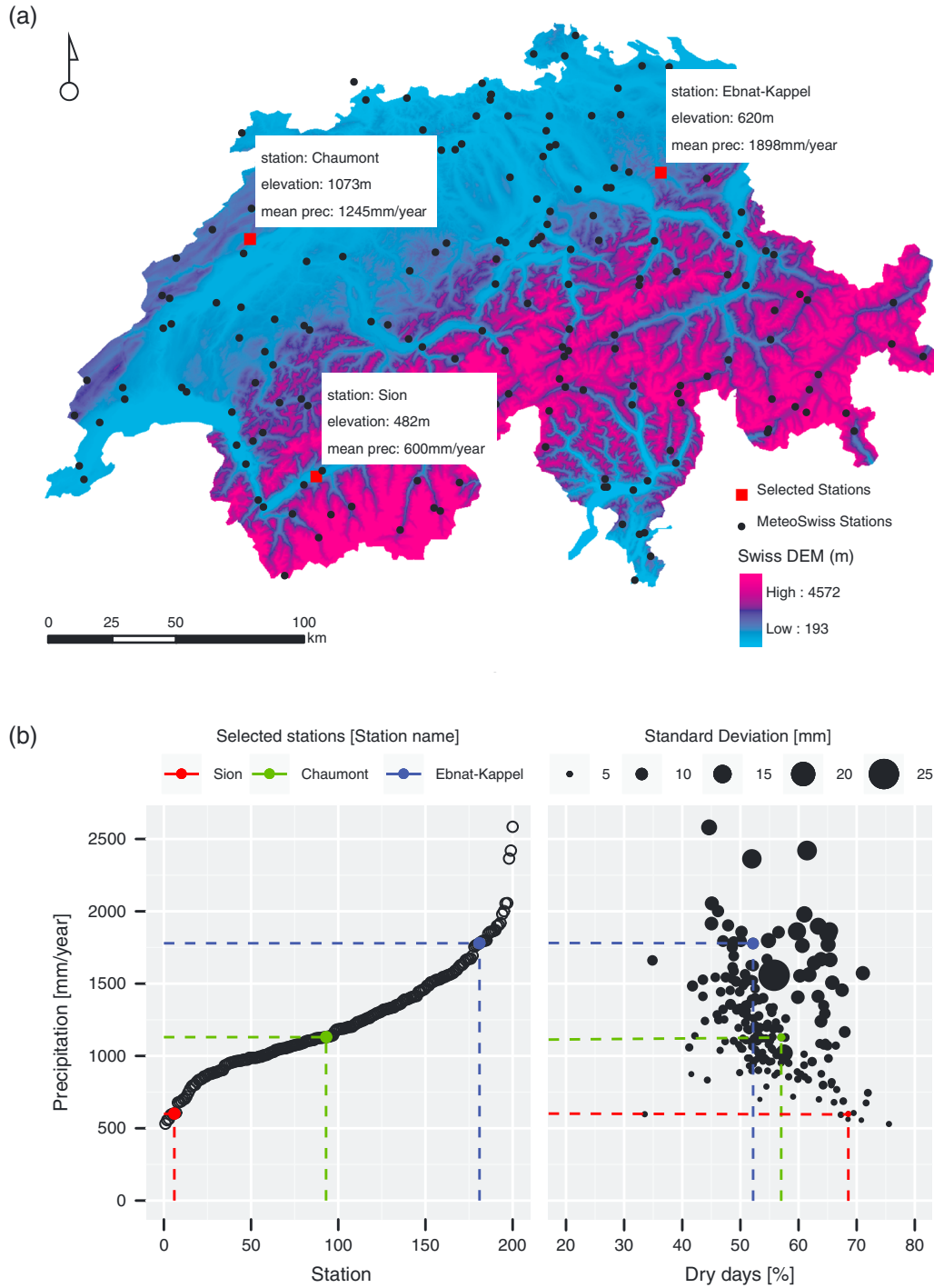
Figure 1. (a) The 200 analyzed meteorological stations in Switzerland with the three selected stations, representative of dry, normal, and wet conditions. (b) Annual statistics, i.e., mean, standard deviation, and percentage of dry days for the investigated stations. The selected stations are highlighted.

2.3.2. Screening Exercise: Elementary Effects

[23] The basic idea of screening approach is based on the Pareto's principle, i.e, model structures tend to have few very influential parameters and a majority of noninfluential ones [*Saltelli et al.*, 2000]. A special case of screening sensitivity analysis is the method of elementary effects (EE) which was originally proposed by *Morris* [1991]. The method is based on individually randomized many one-at-a-time designs. Derivatives with wide range of variation are calculated over the parameter space and their average values are used to provide a global sensitivity metric (see section 1 of the auxiliary material for a detailed description).

[24] The basic statistics, mean (μ_{EE}) and standard deviation (σ_{EE}), of a number of incremental ratios (i.e., EE) are the

Table 3. Detailed Description of the 34 Investigated Parameters and the Process in Which They Are Involved. Their Standard Values as Well as Their Uncertainty Range Based on the Literature Research Is Shown

Process	Parameter	Name	Minimum	Maximum	Standard Values	Units	Description	Reference
Establishment	EST_MAX		0.05	0.48	0.24	indiv m^{-2} yr^{-1}	Maximum sapling establishment rate [Sitch et al., 2003, equation 38]	Zaehle et al. [2005]; Wramneby et al. [2008]
	PARFF_MIN	GRS TBS; NE	300 300	6500 6500	2500 350	kJ m^{-2} d^{-1}	Minimum growing-season forest-floor PAR required for grass growth and tree establishment	Wramneby et al. [2008]
	ALPHA_R		0.1	33.3	3.0	—	Shape parameter for recruitment-juvenile growth rate relationship [Wramneby et al., 2008, equation 1]	Fulton [1991]; Wramneby et al. [2008]
	KEST_BG		0.0	1.0	0.1	—	Empirical parameter for tree establishment rate [Wramneby et al., 2008, equation 1]	Wramneby et al. [2008]
	KEST_REP		15	25	20	—	Empirical parameter for tree establishment rate [Wramneby et al., 2008, equation 1]	Wramneby et al. [2008]
Growth	K_LATOSA	TBS NE	2000 2000	8000 8000	5000 4000	—	Leaf-to-sapwood area ratio [Sitch et al., 2003, equation 1]	Waring and Schroeder, [1982]; Novick et al. [2009]; Zaehle et al. [2005]
	TURN_SAP		0.01	0.20	0.05	frac.yr^{-1}]	Sapwood-heartwood conversion rate [Sitch et al., 2003, equation 27]	Bartelink [1998]; Zaehle et al. [2005]
	LtoR_MAX	GRS TBS; NE	0.1 0.1	5.0 5.0	0.5 1.0	—	Maximum leaf-to-root mass ratio under nonwater-stressed conditions [Sitch et al., 2003, equation 2]	Read et al. [2010]; Sugiura and Tateno [2011]
Mortality	DISTINT		100	500	200	years	Disturbance interval, average return time for generic patch-destroying disturbances	diagnostic
	KMORT_BG		0	3	2	—	Shape parameter for background mortality	Harcombe [1987]; Wramneby et al. [2008]
	GREFF_MIN		0.03	0.18	0.10	kg C m^{-2} leaf yr^{-1}	Threshold for growth suppression mortality	Harcombe [1987]; Pacala et al. [1993]; Wramneby et al. [2008]
	LONGEVITY		100	2100	500	years	Expected maximum life span for 99% of population under nonstressed conditions	Prentice and Helmisaari [1991]; Wramneby et al. [2008]
Soil organic matter	TAU_LITTER		1.23	5.26	2.85	years	Litter turnover time at 10°C	Meentemeyer [1978]; Zaehle et al. [2005]
	ATM_FRAC		0.5	0.9	0.7	—	Fraction of the decomposed litter emitted as CO$_2$ to the atmosphere	Jenkinson et al. 1990; Zaehle et al. [2005]
	FAST_FRAC		0.850	0.990	0.985	—	Fraction of soil-bound decomposed litter entering the intermediate soil pool	Foley [1995]; Zaehle et al. [2005]
Autotrophic respiration	GROWTH_RESP		0.15	0.40	0.25	—	Growth respiration per unit NPP [Sitch et al., 2003, equation 25]	Zaehle et al. [2005]; Wramneby et al. [2008]
Photosynthesis	ALPHA_C3		0.020	0.125	0.080	μmol CO$_2$ μmol^{-1} photons	Intrinsic quantum efficiency of CO$_2$ uptake in C$_3$ plants [Sitch et al., 2003, equation 17]	Farquhar et al. [1980]; Hallgren and Pitman [2000]; Zaehle et al. [2005]
	ALPHA_A		0.3	0.7	0.4	—	Scaling parameter from leaf to canopy accounting for PAR absorbed by nonphotosynthetic structures, thus lost to canopy photosynthesis	Haxeltine and Prentice [1996a,1996b]; Zaehle et al. [2005]
	BC3		0.010	0.021	0.015	—	Leaf respiration as a fraction of Rubisco capacity in C$_3$ plants [Sitch et al., 2003, equation 16]	Farquhar et al. [1980]; Hallgren and Pitman [2000]; Zaehle et al. [2005]

Process	Parameter	PFT				Units	Description	References
	THETA		0.200	0.996	0.700	—	Shape parameter specifing the degree of colimitation by light and Rubisco activity [Sitch et al., 2003, equation 14]	Leverenz [1988]; Collatz et al. [1990]; Zaehle et al. [2005]
	LAMBEER_K		0.4	0.7	0.5	—	Canopy light extinction coefficient [Sitch et al., 2003, equation 7]	Zaehle et al. [2005]
	LAMBDA_MAX		0.6	0.8	0.8	—	Optimal (nonwater-stressed) ratio of intercelural to ambient CO_2 for C_3 plants	Haxeline and Prentice [1996a,1996b]; Zaehle et al. [2005]
AET, EET	GM		2.5	18.5	5.0	$mm\,d^{-1}$	Maximum canopy conductance [Sitch et al., 2003, equation 12]	Magnani et al. [1998]; Zaehle et al. [2005]
	ALPHA_M		1.1	1.5	1.4	—	Empirical evapotranspiration parameter [Sitch et al., 2003, equation 12]	Monteith [1995]; Zaehle et al. [2005]
PET	PR_TAYLOR		1.08	1.60	1.32	—	Priestley-Taylor coefficient, conversion factor from EET to PET	Summer and Jacobs [2005]
Water uptake	EMAX		2.4	6.2	5.0	$mm\,d^{-1}$	Maximum daily transpiration rate	Stewart and Gay [1989]; Whitehead et al. [1994]; Zaehle et al. [2005]
	ROOTDIST	GRS	0.5	1.0	0.8	—	Fraction of fine roots in the upper soil layer	Jackson et al. [1996]; Zaehle et al. [2005]
		TBS; NE	0.5	0.9	0.6			
Demand	GMIN	GRS	0.22	0.58	0.50	$mm\,d^{-1}$	Minimum canopy conductance which accounts for plant-water loss not directly associated with photosynthesis, e.g., cuticular transport [Sitch et al., 2003, equation 21]	Zaehle et al. [2005]
		NE	0.22	0.38	0.30			
		TBS	0.42	0.58	0.50			
Interception	INTC	GRS	0.01	0.2	0.01	—	Rainfall interception coefficient [Gerten et al., 2004, equation 2]	Kergoat [1998]; Gerten et al. [2004]; Zaehle et al. [2005]
		NE	0.01	0.2	0.06			
		TBS	0.01	0.2	0.02			
Hydrology	DEPTH_EVAP		0	500	200	mm	Depth of sublayer at top of upper soil layer from which evaporation is possible	diagnostic
	BASE_FRAC		0.01	0.99	0.50	—	Fraction of precipitation amount from lower soil layer that is diverted to baseflow runoff	diagnostic
	PERC_BASE		0.2	5.0	4.0	$mm\,d^{-1}$	Empirical parameter [Sitch et al., 2003, equation 10]	Sitch et al. [2003]; Gerten et al. [2004]
	PERC_EXP		1	10	2	—	Empirical exponent [Sitch et al., 2003, equation 10]	Neilson [1995]
	SSC		15	450	225	mm	Volumetric water holding capacity (whc) at field capacity minus volumetric whc at wilting point, multiplied by the soil depth	Sitch et al. [2003]

sensitivity measures suggested by *Morris* [1991] for parameter ranking (see section 1 of the auxiliary material for further details). The mean of EE, μ_{EE}, is an estimator of the overall influence of a parameter to the output, and the standard deviation of EE, σ_{EE}, is an indicator of the higher-order parameter effects. The absolute mean value of EE $\left(\mu_{EE}^*\right)$ is used, instead of μ_{EE}, since it is considered as more robust sensitivity metric especially for the case of nonmonotonic functions [*Campolongo et al.*, 2007]. In this study, to facilitate the interpretation of the results and the ranking of parameters, the Euclidian distance, $\epsilon = \sqrt{{\mu_{EE}^*}^2 + \sigma_{EE}^2}$, of $\left(\mu_{EE}^*, \sigma_{EE}\right)$ from the origin (0,0) was used for parameter ranking. In the case of nonlinearities and parameter interactions, this is a fair approximation of the overall parameter sensitivity.

[25] The EE screening test was recursively applied for all the investigated climates to qualitatively assess the relevant importance of each of the 34 parameters. Parameter ranking according to the metric ϵ varies among different output variables and also among different PFTs. An objective selection of the most important parameters was performed using two criteria: (1) the 34 parameters were first ranked according to their mean value of ϵ across the 15 climatic forcings, and then (2) the selection was further restricted by ranking the parameters according to the standard deviation of ϵ. The rational of this classification is that parameters presenting high values of mean ϵ in combination with low standard deviation of ϵ are influential parameters over most climatic scenarios.

[26] While EE method is considered as an accurate and efficient screening test [*Campolongo and Braddock*, 1999; *Campolongo et al.*, 2007], a major drawback is its qualitative character. Since parameters are ranked in terms of relevant importance, no information is provided about how much a given parameter is more important than another or how the different parameters interact [*Saltelli et al.*, 2000, 2004]. Therefore, after a subset of the most influential parameters is identified through the screening test, a detailed variance-based GSA was applied in order to quantify explicitly the importance of, and interactions among, different parameters.

2.3.3. Variance-based Sensitivity Analysis

[27] The Sobol' methodology [*Sobol'*, 1993], a special type of variance-based sensitivity analysis, is applied on the subset of the few most important parameters selected after the qualitative screening exercise (section 2.3.2). The underlying assumption is that all the information about model uncertainty is captured by its variance.

[28] Sobol' sensitivity analysis is based on the traditional Analysis of Variance (ANOVA) [*Archer et al.*, 1997]. In summary, assuming that $Y = f(\mathbf{X})$ is a generalized model and $\mathbf{X} = \{X_1, \ldots, X_k\}$ is a vector of parameters (random variables), where k is the total number of investigated parameters, then the model response, $f(\mathbf{X})$, is decomposed through a functional ANOVA into summands of increasing dimensionality:

$$f(\mathbf{X}) = f(X_1, \ldots, X_k) =$$
$$= f_0 + \sum_{i=1}^{k} f_i(X_i) + \sum_{i=1}^{k}\sum_{j>i}^{k} f_{ij}(X_i, X_j) + \ldots + f_{12\ldots k}(X_1, \ldots, X_k) \quad (1)$$

[29] Note that the following convention is applied in the present work: capital letters are used for random variables,

small letters for their realizations, and bold for vectors and matrices. There are many different ways to decompose $f(\mathbf{X})$ in the form of equation 1, but provided that (1) the vector $\mathbf{X}$ consists of independent parameters, (2) f_0 is a constant ($f_0 = E[Y]$), and (3) all the other terms in equation 1 are selected such that they are square integrable with zero mean, then the decomposition is unique [*Sobol'*, 1993]. Once we square and integrate equation 1, we can partition the total output variance, V_Y, into terms of increasing dimensionality:

$$V_Y = V[Y] = V[f(\mathbf{X})] = \sum_i^k V_i + \sum_{i=1}^{k}\sum_{j>i}^{k} V_{ij} + \cdots + V_{12\ldots k} \quad (2)$$

where $V_i = V\left[E\left[Y|X_i = x_i^*\right]\right]$, $V_{ij} = V\left[E\left[Y|X_i = x_i^*, X_j = x_j^*\right]\right] - V_i - V_j$, and so on. $E[\cdot|\cdot]$ is the conditional expectation, and x_i^*, x_j^* denote the *real* values of the parameters i and j, respectively. In other words, similar to the ANOVA concept, the total output variance is partitioned to different subcomponents which contribute to the overall output variability [*Archer et al.*, 1997; *Chen et al.*, 2005].

[30] The sensitivity indices are then derived as the ratios of partial variances contributed by specific parameters of interest over the total output variance:

$$1 = \sum_i^k S_i + \sum_{i=1}^{k}\sum_{j>i}^{k} S_{ij} + \ldots + S_{12\ldots k} \quad (3)$$

where S_i is the first-order sensitivity index (or main effect) of the ith parameter, S_{ij} is the second-order sensitivity index which represents the interactions of the ith and jth parameters, and so on. Accordingly, the total sensitivity index, S_{Ti}, which represents the overall parameter importance (first- and higher-order effects), for the orthogonal case (i.e., independent parameters) is the sum of all the sensitivity indices of equation 3 that include the ith parameter [*Saltelli et al.*, 2004]. The first- and total-order sensitivity indices are estimated since they include the most essential information and they offer a robust estimation of parameter importance and interactions [*Homma and Saltelli*, 1996; *Saltelli*, 2002].

[31] The first-order sensitivity index of parameter X_i is defined as

$$S_i = \frac{V_i}{V_Y} = \frac{V[E[Y|X_i]]}{V[Y]} \quad (4)$$

[32] The variance of the conditional expectation $V[E[Y|X_i]]$ represents the expected variance reduction that could be achieved when X_i would become perfectly known (i.e., $X_i = x_i^*$). The expectation of model response Y over the entire variation interval of X_i (i.e., $E[Y|X_i]$) is used since we are not able to know the *real* value x_i^* for each parameter X_i. First-order sensitivity indices represent the main effect contribution of individual parameters to the output variance [*Saltelli et al.*, 2008] and are therefore considered an agile measure for sensitivity assessments, but they are not enough for a rigorous GSA because quantification of higher-order effects can also be important [*Chan et al.*, 1997].

[33] Total-order sensitivity indices attempt to bridge this gap by estimating not only first- but also higher-order effects. According to variance decomposition presented in equation 2,
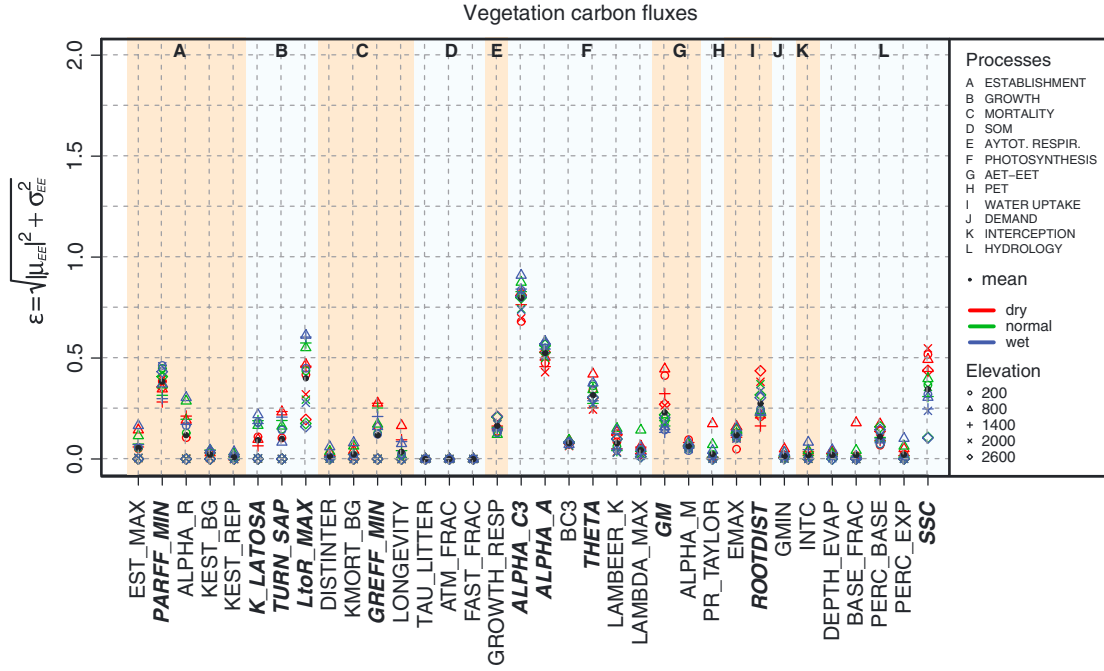
Figure 2. Qualitative results of the screening analysis for total NPP (i.e., vegetation carbon fluxes). The sensitivity metric ϵ under different climate conditions is illustrated. The 11 parameters selected for the detailed analysis are highlighted with bold italic characters.

the total effect index of the ith parameter can be expressed as
$$S_{Ti} = S_i + \sum_{j \neq i}^{k} S_{ij} + \cdots + S_{12\ldots k}$$
and it is defined as

$$S_{Ti} = \frac{E[V[Y|\mathbf{X}_{\sim i}]]}{V[Y]} = 1 - \frac{V[E[Y|\mathbf{X}_{\sim i}]]}{V[Y]} \quad (5)$$

where $\mathbf{X}_{\sim i}$ is a vector of all the random variables (i.e., parameters) but the ith. The term $E[V[Y|\mathbf{X}_{\sim i}]]$ is the expected amount of variance that would remain unexplained if X_i, and only X_i, were left free to vary over its uncertainty range, all the other parameters (i.e., the vector $\mathbf{X}_{\sim i}$) having been learnt [*Homma and Saltelli*, 1996; *Saltelli et al.*, 2008]. Similarly to the main effect, the outer expectation is used since the *true* values of the $\mathbf{X}_{\sim i}$ vector are not known.
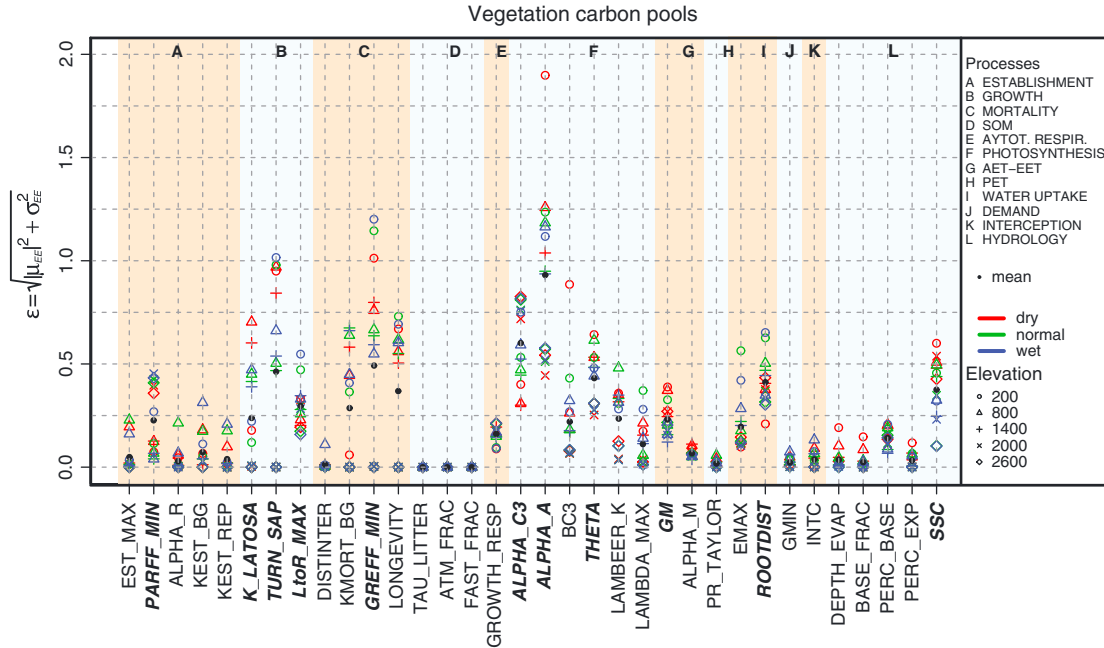
Figure 3. Qualitative results of the screening analysis for total vegetation biomass (i.e., vegetation carbon pools). The sensitivity metric ϵ under different climate conditions is illustrated. The 11 parameters selected for the detailed analysis are highlighted with bold italic characters.

Table 4. The 11 Parameters Selected Through the Screening Test, Categorized in Terms of Simulated Processes

Process	Parameters
Vegetation establishment	*PARFF_MIN*
Plant growth and structure	*K_LATOSA*
	TURN_SAP
	LtoR_MAX
Photosynthesis	*ALPHA_C3*
	ALPHA_A
	THETA
Mortality	*GREFF_MIN*
Transpiration	*GM*
Water uptake	*ROOTDIST*
Soil hydrology	*SSC*

Total effect indices play a pivotal role in distilling information about the overall parameter importance since they highlight nonadditive features of the model structure and allow one to quantify parameter interactions, by subtracting the first order from the total sensitivity indices.

[34] A detailed description of the implemented computational scheme is available in section 2 of the auxiliary material. In summary, for estimating first and total sensitivity indices, the computational strategy originally proposed by

Sobol' [1993] and further improved by *Saltelli* [2002] and *Saltelli et al.* [2010] was followed. A convergence test was also conducted for defining the number of necessary model evaluations (6656 model runs were selected, see details in section 4 of the auxiliary material). The sampling strategy is based on the Sobol' low discrepancy sequences, LP_τ sequences [*Sobol'*, 1967, 1976], because they provide an enhanced convergence rate of the numerical estimators [*Chan et al.*, 2000; *Saltelli et al.*, 2000, 2004, 2008, 2010]. A better description of LP_τ appealing properties is provided in section 3 of the auxiliary material.

3. Results

3.1. Screening Results

[35] The sensitivity metric ϵ gives comparable ranking of the parameters for the case of vegetation biomass and NPP. Parameters that exert high sensitivity for NPP also do so for vegetation biomass (Figures 2 and 3). The variability in the parameter sensitivity induced by different climate forcings is generally lower in comparison to the variability induced by the parameters themselves. A subset of 11 potentially critical parameters was identified according to the ϵ-based ranking
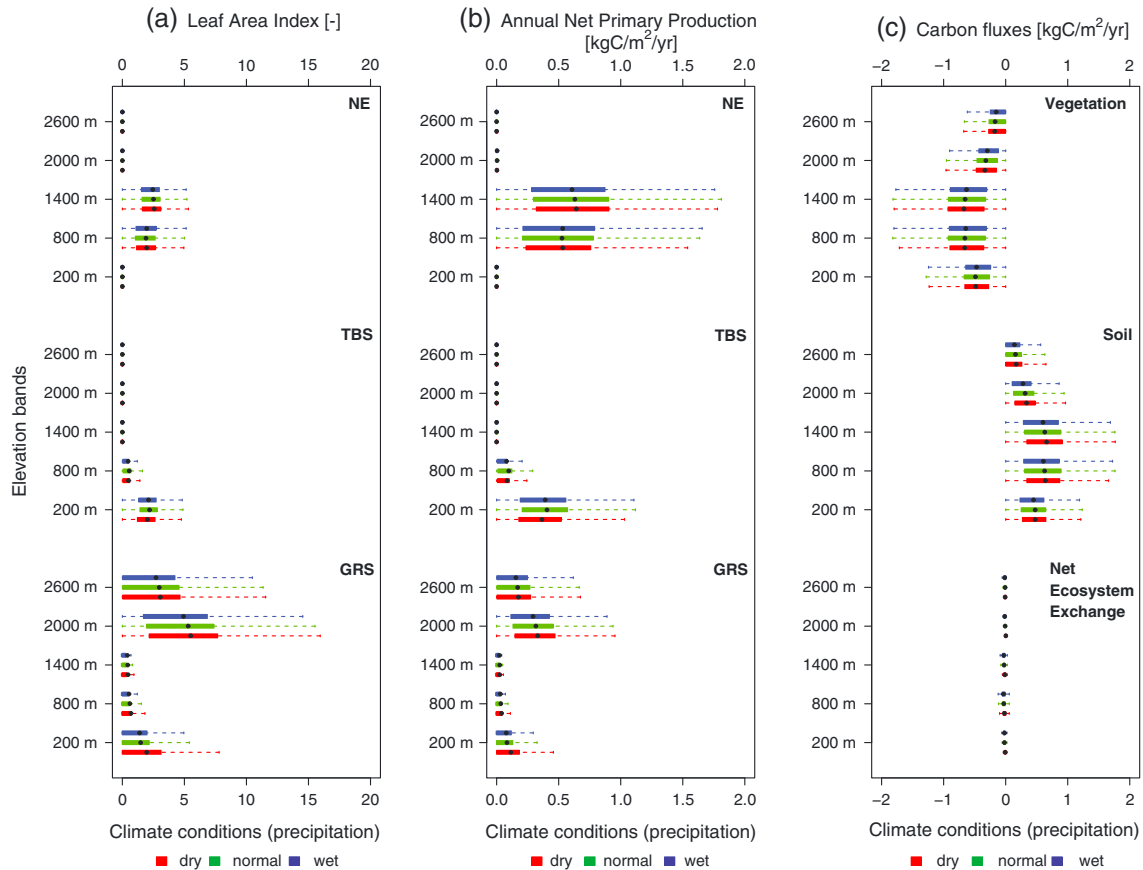
Figure 4. Distribution of LAI, NPP, and carbon fluxes for different climatic forcings (from wet to dry conditions and from low to high elevations), when the 11 selected parameters were varied simultaneously (6656 model evaluations). (a) LAI, (b) annual NPP, and (c) carbon fluxes for the different ecosystem components are presented. Boxes are extended from 25% lower quartile ($q_{0.25}$) to 75% upper quartile ($q_{0.75}$) while whiskers represent the range of $[q_{0.5} - 1.5IQR, q_{0.5} + 1.5IQR]$, where $q_{0.5}$ is the median and *IQR* is the interquartile range ($q_{0.75} - q_{0.25}$).

(Figures 2 and 3 and Table 4). The parameter selection was also corroborated by an analysis of other complementary output variables such as LAI (results not shown).

[36] From the screening emerges that vegetation carbon assimilation and fluxes show low sensitivity to hydrological parameters that define and regulate directly or indirectly the available soil water to plants. Parameters related to the terrestrial water balance, such as runoff generation (*BASEFLOW_FRAC*) and percolation (*PERC_BASE*, *PERC_EXP*) have no important effect on the variability of vegetation carbon fluxes and pools, especially when compared to biochemical or biophysical parameters (Figures 2 and 3). Only soil texture properties, specifically SSC, defined as the difference between volumetric water content at field capacity and volumetric water content at wilting point multiplied by soil depth is found important. It occurs as the only parameter related to the terrestrial water balance that might significantly influence vegetation carbon sequestration.

[37] In accordance with Pareto's principle (section 2.3.2), only 11 parameters, out of 34 originally examined, were selected after the EE screening analysis (Table 4). The importance of these parameters was further investigated by applying a detailed variance-based GSA.

3.2. Results of Variance-based Sensitivity Analyses

3.2.1. First and Total Sobol' Sensitivity Indices

[38] The distribution of model outputs (mean values over the 44 year historical period) for the 6656 model simulations, where the 11 parameters were varied simultaneously, under different climatic forcings is illustrated in Figure 4.

The annual NPP of each PFT (Figure 4b) facilitates the delineation of stand composition in terms of dominant and subdominant PFTs. In our study, evergreen trees can be found between 800 and 1400 m asl while deciduous trees occur from 200 to 800 m asl of elevation. The simulated herbaceous PFT occurs at all the elevation bands and for high elevations (2000 and 2600 m asl) dominates the entire stand, without any woody PFT being present.

[39] About 50%–70% (according to the climate forcing) of the variability in the total annual NPP is explained by the uncertainty of *ALPHA_C*3. Most of this variability is caused by first-order effects (40%–60%) while only 10% is due to interactions with other parameters (Figure 5). *ALPHA_C*3 is the parameter that regulates the initial slope of the light response curve of photosynthesis, representing the maximum efficiency of incident light-energy conversion, i.e., light utilization [*Haxeltine and Prentice*, 1996a, 1996b; *Wohlfahrt et al.*, 1999; *von Caemmerer*, 2000; *Singsaas et al.*, 2001; *Gates*, 2003; *Bonan*, 2008a]. The high sensitivity to *ALPHA_C*3 is consistent through the examined precipitation conditions (from dry to wet climates) but shows a certain variability across elevation bands due to variability in vegetation composition (Figure 4). At high elevations, e.g., 2600 m asl, where grass dominates the simulated stand, the importance of *ALPHA_C*3 is lower than at 800 m asl, where woody and herbaceous PFTs coexist and compete. The second most influential parameter for vegetation carbon fluxes is *ALPHA_A*, i.e., the scaling parameter from leaf to canopy. Roughly 20% of output variability is due to the uncertainty of *ALPHA_A*. The influence of *ALPHA_A* in the variability of NPP is relatively constant across the examined
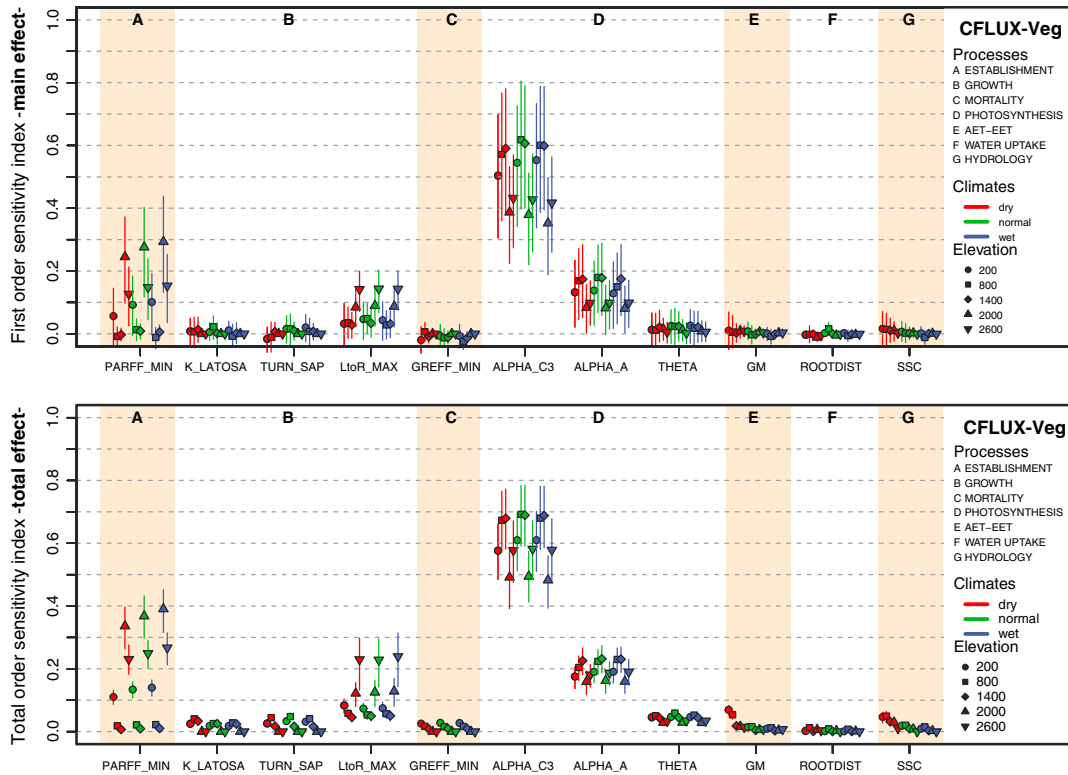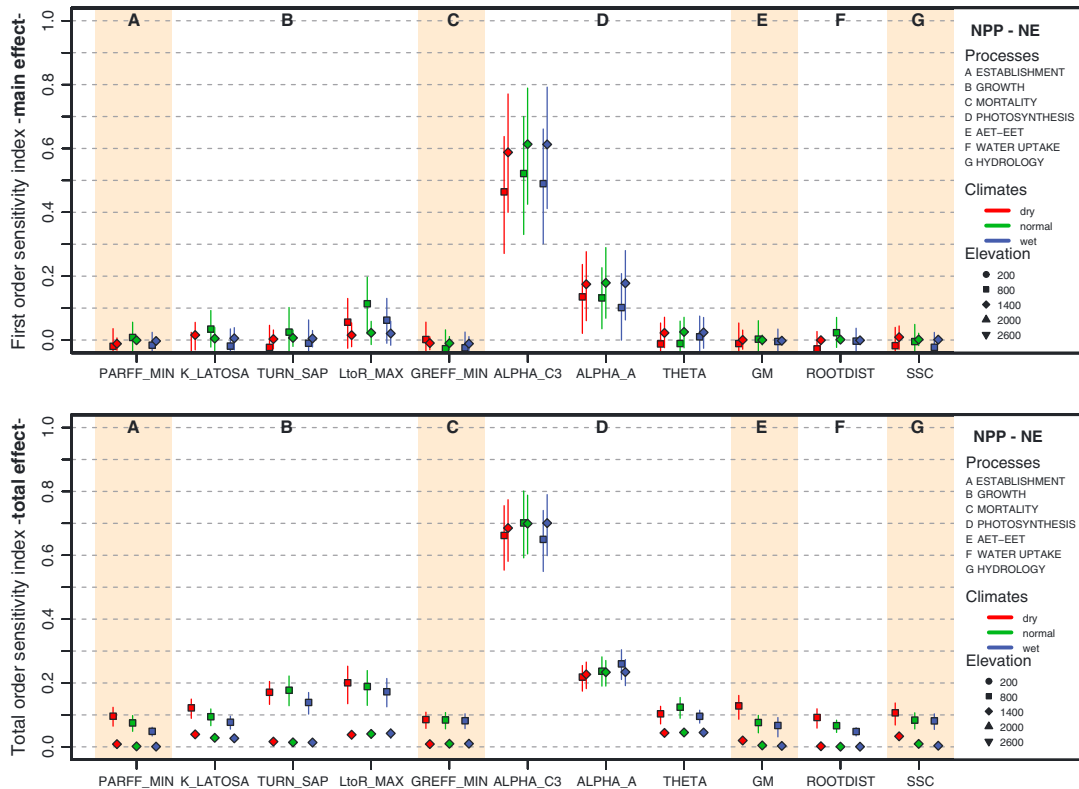

Figure 5. First and total Sobol' sensitivity indices of the 11 investigated parameters with their 95% confidence intervals (vertical lines), for vegetation stand NPP under different climate forcings (from wet to dry conditions and from low to high elevations).

environmental conditions. Since *ALPHA_C3* and *ALPHA_A* regulate the efficiency in converting solar radiation to carbon, they essentially control vegetation carbon fluxes, causing high variability in model outputs. The parameter *PARFF_MIN*, which determines establishment for woody, and growth for herbaceous PFTs, is also a crucial parameter at high elevation (2000–2600 m asl), where grass tends to dominate the simulated stand. At the elevation band of 2000 m, where grass is abundant, around 40% of the variability in vegetation carbon fluxes is due to the first-order effect of *ALPHA_C3*, while around 30% is induced by the first-order effect of *PARFF_MIN*. At the highest elevation (2600 m asl), where grass is the only occurring PFT, *ALPHA_C3* is again the most influential parameter, accounting for 60% of variability in the simulated NPP, of which about 40% is due to first order effects, while 20% is due to interactions with other parameters. In this non competitive environment dominated by grass, *LtoR_MAX*, which affects the partition of below-ground and above ground biomass, is of similar importance as *PARFF_MIN* and *ALPHA_A*, causing around 25% of variability in the vegetation carbon fluxes, out of which 10% is due to interactions.

[40] Since there is ample evidence that patch composition affects the model results (e.g., the performance of the simulated biomes) and therefore the parameter importance [*Tilman et al.*, 1997; *Wramneby et al.*, 2008], we examined the effects of parameter uncertainty in the simulated NPP separately for each PFT (Figures 6–8).

[41] Comparing parameter sensitivity of the two woody PFTs, coniferous evergreen (Figure 6) and broadleaf deciduous (Figure 7), we can highlight different sensitivity patterns. When competition among PFTs occurs, the model shows sensitivity to additional parameters since higher-order effects start playing a more important role for the model outcomes. This is particularly evident in Figures 6 and 7 where parameters related to plant structure are becoming significantly important in terms of total effects while their first-order indices are relatively low, underlining the effect of parameter interactions. At 800 m asl elevation, where evergreen and deciduous trees coexist and compete for the same resources, parameters related to plant growth and structure (*TURN_SAP*, *LtoR_MAX*) are becoming influential for evergreen trees (Figure 6). Deciduous trees (Figure 7), that are subdominant at this elevation, i.e., they have a significantly lower productivity in comparison to evergreens, show sensitivity to many parameters controlling their occurrence and growth (e.g., *ALPHA_C3*, *K_LATOSA*, *TURN_SAP*, *LtoR_MAX*, *GREFF_MIN*) especially in terms of higher-order effects.

[42] The sensitivity of the productivity of grass is also influenced by stand composition. At low and middle elevations (200–1400 m asl), where woody and herbaceous PFTs coexist, the productivity of grass is mostly sensitive to *PARFF_MIN*, which defines a light threshold required for grass to grow (Figure 8). Due to tree shadowing effects, the available photosynthetically active radiation (PAR) is reduced and *PARFF_MIN* becomes very critical for the

Figure 6. First and total Sobol' sensitivity indices of the 11 investigated parameters for the NPP of needle-leaved trees under different climate forcings (from wet to dry conditions and from low to high elevations). The 95% confidence intervals are also plotted (vertical lines). Constrained by the ascribed bioclimatic limits, needle-leaved vegetation occurs only between 800 and 1400 m asl elevation.
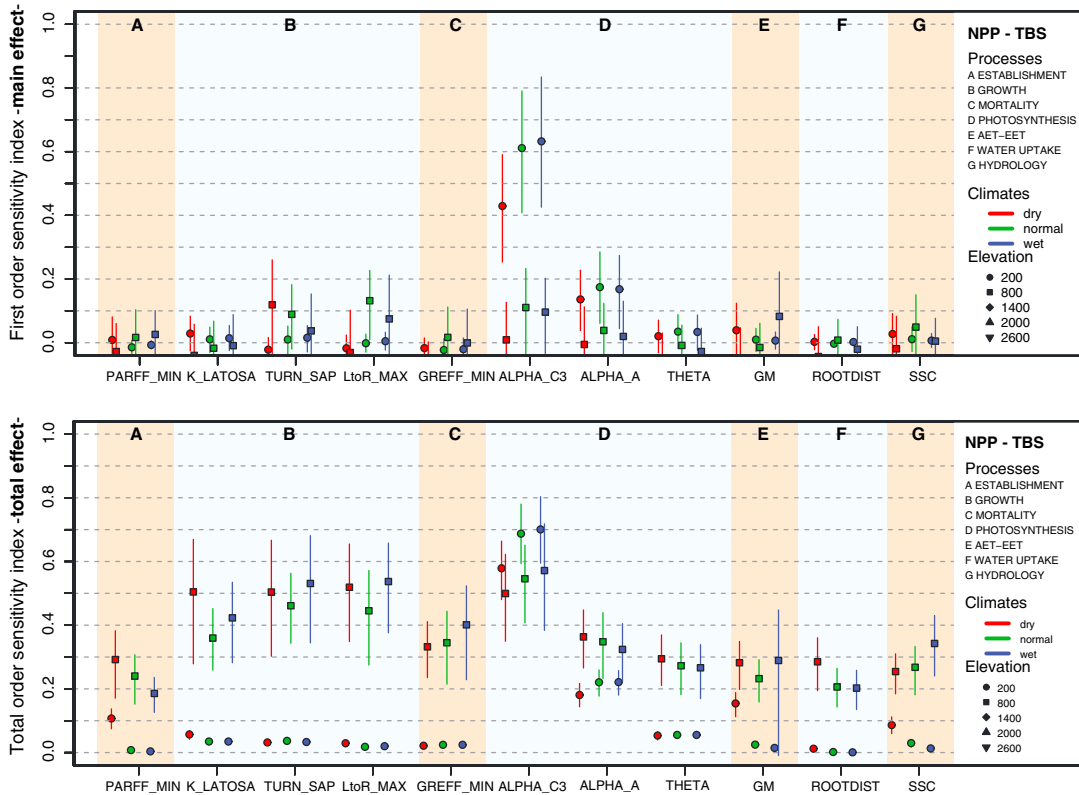
Figure 7. First and total Sobol' sensitivity indices of the 11 investigated parameters for the NPP of broad-leaved trees under different climate forcings (from wet to dry conditions and from low to high elevations). The 95% confidence intervals are also plotted (vertical lines). Constrained by the ascribed bioclimatic limits, broad-leaved vegetation occurs only between 200 and 800 m asl elevation.

productivity of grass. The second most influential parameter, responsible for around 30% of the variance in the simulated NPP of grass, is the maximum leaf-to-root mass ratio (*LtoR_MAX*). At higher elevations where grass does not compete with woody PFTs, the importance of *PARFF_MIN* and *LtoR_MAX* significantly decreases. Contemporaneously, intrinsic quantum efficiency becomes the most sensitive parameter, explaining about 50%–60% of the grass NPP variability (Figure 8).

[43] Finally, intrinsic quantum efficiency is confirmed to be the most important parameter for the total carbon stored by vegetation under all the climate forcings (Figure 9), independent of patch composition. *ALPHA_C*3 alone explains 50%–60% of the variability in the vegetation carbon pools. *ALPHA_A* also shows a consistent influence on the output variability across all the elevation bands with a total-order effect of ≈ 0.2. However, the second most important parameter for the carbon stored in vegetation pools, when simulated stand is occupied by woody PFTs (200–1400 m asl elevation), is *TURN_SAP*, which defines the conversion rate between sapwood and heartwood. At high elevations, where grass occupies the entire tile, *PARFF_MIN* becomes the second most important parameter after *ALPHA_C*3.

3.2.2. Sobol' GSA Excluding Photosynthesis-Related Parameters

[44] The strong sensitivity of LPJ-GUESS to the parameterization of photosynthesis scheme may hide the importance of other parameters and processes. Thus, in order to consolidate our findings and investigate any potential damping

effect in the parameter ranking caused by the overwhelming contribution of intrinsic quantum efficiency, we repeated the GSA by excluding parameters related to photosynthesis. Specifically, *ALPHA_C*3, *ALPHA_A*, and *THETA* were fixed to their standard values (Table 3), and the first and the total Sobol' sensitivity indices were calculated for the eight remaining parameters. By excluding the photosynthesis parameters, the importance of light harvesting and plant-structure parameterization were further scrutinized and the low sensitivity of soil water content was also reconfirmed.

[45] Figure 10 shows the distribution of the 44 year average values of LAI, NPP, and carbon fluxes. The stand composition is similar as in Figure 4, where photosynthesis parameters were included in the analysis. However, the distribution of the output is narrower and with less dispersion. There is no important variation in the examined output and stand composition with the different precipitation patterns (Figure 10), i.e., Sobol' sensitivity indices are similar under dry, normal, and wet conditions. Therefore, results are illustrated only for the case of normal precipitation forcing (Figures 11 and 12). Coxcomb plots, which are essentially bar charts in polar coordinates, were used to summarize the parameter ranking of the different stand compositions. Total Sobol' sensitivity indices of the examined parameters are depicted for the elevation bands where each PFT is predominant in the simulated stand (TBS at 200, NE at 1400, and GRS at 2000 m asl) and for the elevation band of 800 m asl, where all the PFTs coexist and compete (Figures 11 and 12).
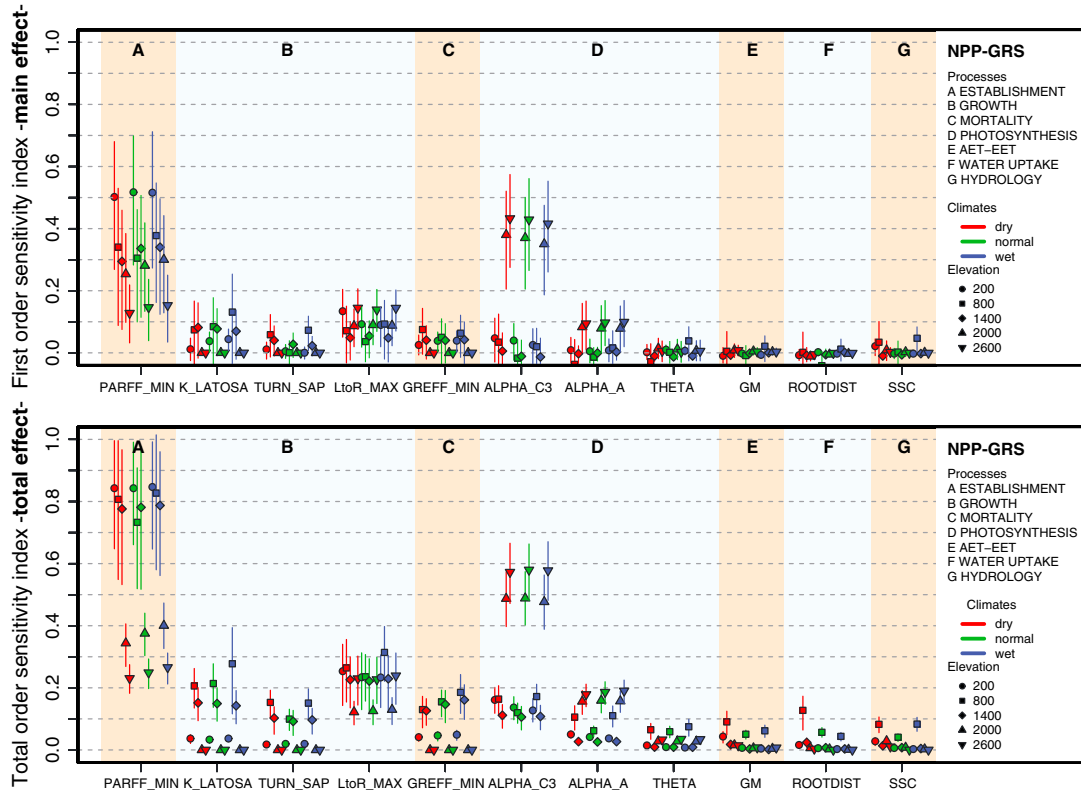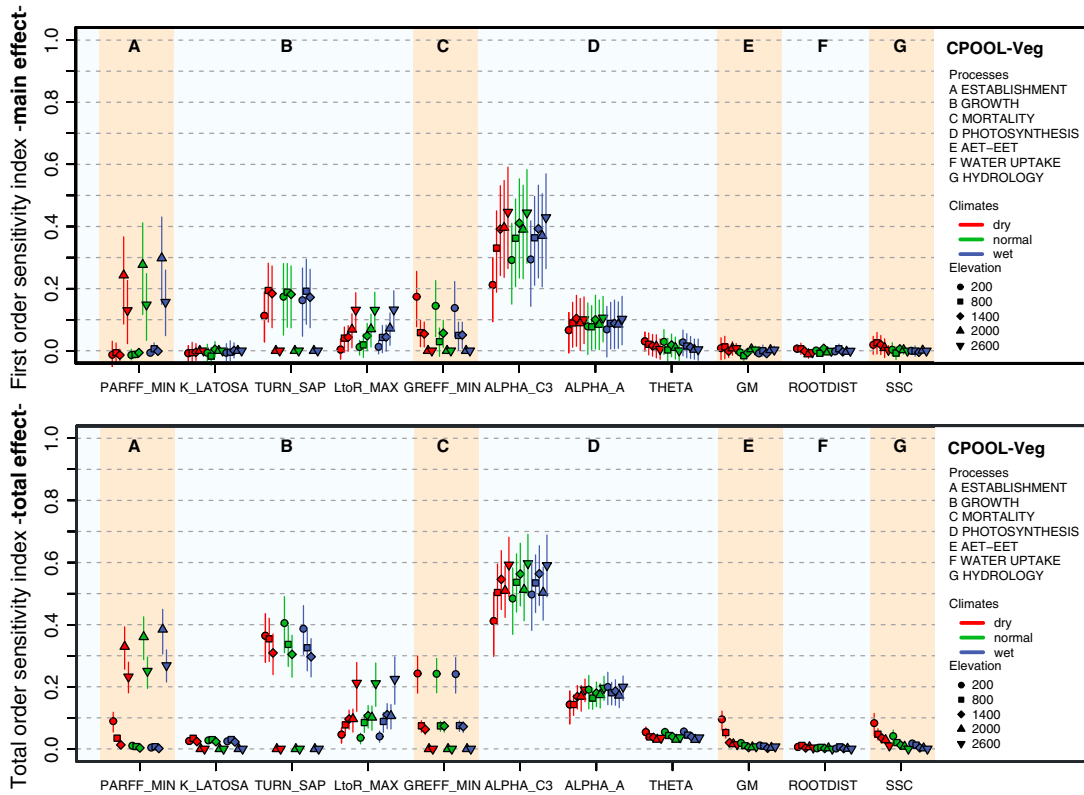
Figure 8. First and total Sobol' sensitivity indices of the 11 investigated parameters for the NPP of grass, under different climate forcings (from wet to dry conditions and from low to high elevations). The 95% confidence intervals are also plotted (vertical lines).

[46] The parameter *LtoR_MAX* is found to be very important for the vegetation carbon fluxes, independent of stand composition (Figures 11a and 11b). At the elevation of 200 m asl where TBS is the dominant PFT, *PARFF_MIN* is the most important parameter explaining 60% of the variability in NPP and *LtoR_MAX* is the second most important with a total-order sensitivity index ≈ 0.4. At 2000 m asl, where the entire stand is covered by grass, the sensitivity patterns are similar, *PARFF_MIN* explains most of the variability in vegetation carbon fluxes, and *LtoR_MAX* is the second most important parameter. At the elevation of 800 m asl, where the two woody PFTs and grass coexist (NE is the dominant PFT and TBS the subdominant), *LtoR_MAX* is the most critical parameter, with a total-order sensitivity index ≈ 0.6.

[47] For the vegetation biomass (vegetation carbon pools, Figures 11c and 11d), parameters regulating plant structure and mortality, *TURN_SAP* and *GREFF_MIN* respectively, are the most important parameters for the elevation bands where woody PFTs are dominant (200–1400 m asl). *GREFF_MIN* is the most sensitive parameter for vegetation carbon pools when only TBS trees occur and *TURN_SAP* is the second most important. For stands with only NE trees, *TURN_SAP* is the most sensitive parameter and *GREFF_MIN* is the second most sensitive. When grass is the only PFT that occurs in the simulated stand, *PARFF_MIN* is found to be the most important parameter (Figure 11c). At the elevation of 800 m asl, *TURN_SAP*, *GREFF_MIN*, and *LtoR_MAX* emerge as the most influential parameters, as a result of the coexistence of different PFTs.

[48] Summarizing, despite some differences due to stand composition, the parameter ranking is fairly similar for the vegetation carbon fluxes and pools under the entire spectrum of the used climate forcings. *PARFF_MIN* and *LtoR_MAX* are the most influential parameters for NPP under all the examined stand compositions. For the vegetation carbon pools, *TURN_SAP*, *GREFF_MIN*, and *LtoR_MAX* are the three key parameters when woody PFTs occur. When the simulated stand is only covered by herbaceous species, *PARFF_MIN* is the most important parameter.

[49] Contrary to what we found for vegetation carbon fluxes and pools, the sensitivity metrics at the PFT level, e.g., NPP and LAI of each specific PFT, are strongly conditioned by stand composition. Total sensitivity indices for NPP and LAI of the eight examined parameters of NE, TBS, and GRS are illustrated in Figure 12 for the different stand compositions and normal precipitation conditions. When only one PFT occurs in the simulated stand, there are very few parameters that essentially affect the PFT specific model outputs (Figures 12a and 12c), while at the 800 m asl elevation band where all the simulated PFTs coexist, many parameters become influential, affecting NPP and LAI of each PFTs (Figures 12b and 12d). When woody PFTs occupy the entire stand, *K_LATOSA* and *LtoR_MAX* are of paramount importance. However, the examination of elevation bands where competition among PFTs takes place, led to the identification of additional crucial parameters. Especially for broad-leaved trees, which are subdominant at 800 m asl, the total sensitivity indices of most of the parameters are higher when compared to needle-leaved trees

Figure 9. First and total Sobol' sensitivity indices of the 11 investigated parameters with their 95% confidence intervals (vertical lines) for the vegetation carbon pools (sum of the carbon allocated in leaves, sapwood, heartwood, and fine roots) under different climate forcings.

that dominate the forest stand. For grass, *PARFF _ MIN* is the most sensitive parameter independent of forest stand composition, but the sensitivity is higher in the presence of trees. Trees reduce the amount of radiation that penetrates the canopy and reaches the forest floor and thus, light becomes the limiting factor for grass growth. Grass is also strongly influenced by the maximum leaf-to-root mass ratio (*LtoR _ MAX*), especially at high elevations.

4. Discussion

[50] The results described in the previous sections provide a thorough evaluation of LPJ-GUESS terrestrial ecosystem model. For the first time, advanced sensitivity analysis methodologies are applied to a DGVM not only for estimating the sensitivity to different parameters but also for better understanding the importance of the model structure. Since it is widely accepted that mimicking the reality should imply more than a simple agreement with observed variables [*Weisberg*, 2007], especially when long-term or climate nonstationary quantitative predictions are envisioned [*Cox et al.*, 2006; *Evans*, 2012], such a type of model evaluation is fundamental.

4.1. Sensitivity to Photosynthesis and Plant Growth

[51] The Farquhar photosynthesis scheme [*Farquhar et al.*, 1980; *Collatz et al.*, 1991] turned out to include the most sensitive out of the 34 examined model parameters of LPJ-GUESS, in particular the intrinsic quantum efficiency. In agreement with the results of *Zaehle et al.* [2005],

intrinsic quantum efficiency is of utmost importance in the LPJ-GUESS parameterization, explaining most of the variability in vegetation carbon fluxes and pools, regardless of stand composition and climate forcings. The essential role of photosynthesis parameterization in controlling the terrestrial ecosystem carbon budget has also been detected in other modeling studies [*Hallgren and Pitman*, 2000; *Medlyn et al.*, 2005; *Zaehle et al.*, 2005; *Alton et al.*, 2007; *Matthews et al.*, 2007; *Chen et al.*, 2011; *Bonan et al.*, 2011; *Dietze et al.*, 2011]. Specifically, the maximum capacity for carboxylation has been found to be a key plant physiological parameter which can strongly influence not only photosynthesis but also the global climate [*Bonan et al.*, 2011].

[52] This critical role of the process of photosynthesis in controlling long-term vegetation carbon fluxes and pools (responsible for about 60% of the output variability in the case of LPJ-GUESS) is contradicted by field experiments, which suggest that photosynthesis may be a consequence rather than a driver of plant growth [*Körner*, 2003; *Zweifel et al.*, 2006; *Muller et al.*, 2011; *Hoch and Körner*, 2012]. Thus, the generally simplistic and mostly static carbon allocation schemes of DGVMs [e.g., *Shinozaki et al.*, 1964; *Huang et al.*, 1992; *Zeide*, 1993] create high sensitivity of plant growth to photosynthesis, neglecting processes such as direct growth limitation by temperature [*Oberhuber et al.*, 2011; *Hoch and Körner*, 2012; *Körner*, 2012] or water [*Würth et al.*, 1998; *Muller et al.*, 2011]. We acknowledge the fundamental role of photosynthesis in controlling short-term carbon fluxes and in this regard, more accurate representations of canopy layers, leaf temperature, and light
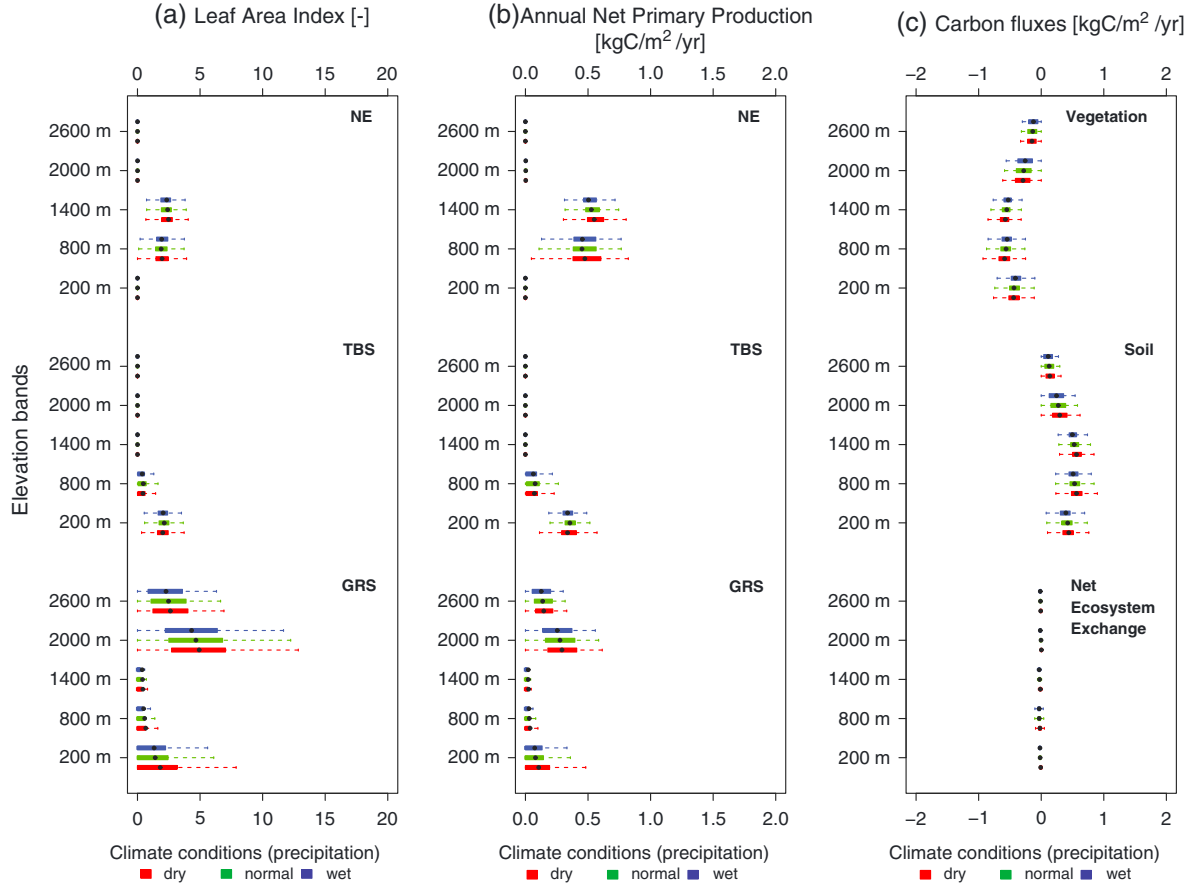
Figure 10. Distribution of LAI, NPP, and carbon fluxes for different climatic forcings, when the eight remaining parameters, after removing photosynthesis parameterization from the GSA, were varied simultaneously (5120 model evaluations). (a) LAI, (b) annual NPP, and (c) carbon fluxes for the different ecosystem components are presented. Boxes are extended from 25% lower quartile ($q_{0.25}$) to 75% upper quartile ($q_{0.75}$) while whiskers represent the range of $[q_{0.5} - 1.5IQR, q_{0.5} + 1.5IQR]$, where $q_{0.5}$ is the median and IQR is the interquartile range ($q_{0.75} - q_{0.25}$).

harvesting can be very important [e.g., *De Pury and Faruhar*, 1997; *Dai et al.*, 2004; *Kobayashi et al.*, 2012]. However, we underline that forest growth and development (and therefore long-term carbon fluxes) result from complex interactions and should not be dominated by the process of photosynthesis. For instance, the importance of plant structure and architecture in determining carbon assimilation has been recognized recently [*Luyssaert et al.*, 2008; *Ishii and Asano*, 2010; *Hardiman et al.*, 2011] and is confirmed by our GSA with fixed photosynthesis parameters. Overall, we suggest that these contradictions call for a more mechanistic representation of carbon allocation and translocation (e.g., carbon sink rather than carbon source driven, *Leuzinger et al.* [2013]) and it represents one of the key challenges for future model improvements [*Hurtt et al.*, 1998; *Daudet et al.*, 2002; *Litton et al.*, 2007; *Fisher et al.*, 2010; *De Schepper and Steppe*, 2011; *Franklin et al.*, 2012; *Mäkelä*, 2012; *Sala et al.*, 2012].

4.2. Photosynthesis in the LPJ Model Family

[53] LPJ-GUESS (as well as LPJ-DGVM) originates from the BIOME model family [*Prentice et al.*, 1992; *Haxeltine and Prentice*, 1996a; *Haxeltine et al.*, 1996]. In these models, the implemented photosynthesis scheme, for both C_3 and C_4 species, is based on a simplified mechanistic approach [*Farquhar et al.*, 1980; *Collatz et al.*, 1991, 1992], which allows for an analytical solution as demonstrated by *Haxeltine and Prentice* [1996a, 1996b] and *Haxeltine et al.* [1996]. Net photosynthesis and stomatal conductance are calculated at a daily time scale using a nonrectangular hyperbola formulation describing the transition between light-limited and Rubisco-limited photosynthesis rates [*Haxeltine and Prentice*, 1996b; *Cannell and Thornley*, 1998]. However, the analytical expressions of daily photosynthesis emerge from the assumption that for any PAR level, there is an optimal photosynthetic enzyme activity that maximizes net photosynthesis [*Haxeltine and Prentice*, 1996a, 1996b]. Specifically, the canopy-average maximum Rubisco capacity (V_{max}) of each simulated average individual is not predefined, as it is required by the original Farquhar photosynthesis scheme and implemented in other models [e.g., *Knorr*, 2000; *Krinner et al.*, 2005; *Bonan et al.*, 2011; *Ivanov et al.*, 2008a; *Fatichi et al.*, 2012a], but it is adjusted daily in an optimal way, under the assumption that leaf nitrogen distribution through the canopy maximizes daily canopy net assimilation. This optimality
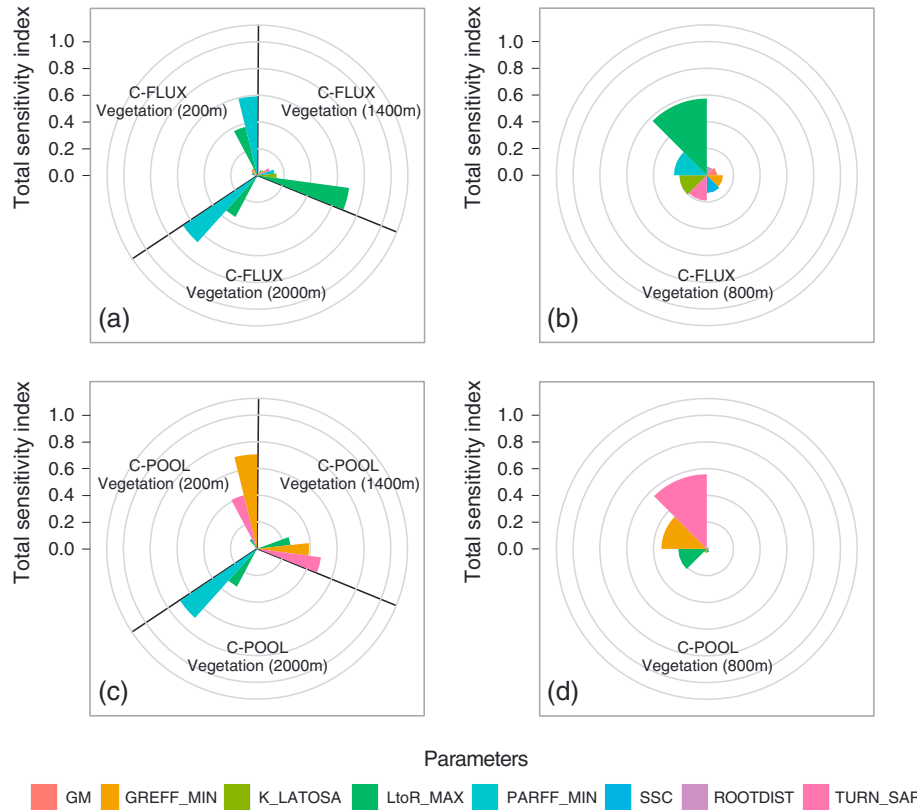
Figure 11. Coxcomb plots of the total effect sensitivity indices for (a and b) vegetation carbon fluxes and (c and d) vegetation carbon pools. Total effect sensitivity indices are reported for the three different elevation bands where each of the simulated PFT is the dominant (TBS at 200 m asl, NE at 1400 m asl, and GRS at 2000 m asl) under normal precipitation conditions (in Figures 11a and 11c), as well as for the elevation band of 800 m asl where all the PFTs coexist (in Figures 11b and 11d)

constraint is likely responsible for the strong sensitivity of LPJ-GUESS to $ALPHA\_C3$. In LPJ-GUESS, $ALPHA\_C3$ represents more than intrinsic quantum efficiency and does not only affect the light-induced carbon fixation [*Haxeltine and Prentice*, 1996a, equations 2 and 4]. Therefore, variations in $ALPHA\_C3$ indirectly affect the optimized value of V_{max} [*Haxeltine and Prentice*, 1996a, equation 11], and this sequentially affects the Rubisco-limited assimilation [*Haxeltine and Prentice*, 1996a, equation 5]. In other words, the optimization procedure, applied for obtaining analytical solutions of daily photosynthesis, implies that the uncertainty originally attributed to the intrinsic quantum efficiency also reflects the uncertainty propagated by the internal adjustment of V_{max}. Therefore, the biochemical processes of photosynthesis and specifically the light use efficiency of plants (mediated by the intrinsic quantum efficiency parameter and entailing V_{max} variation as well) are found to be the cornerstones of LPJ-GUESS framework.

[54] Given the computational cost of concurrently solving processes involved in plant photosynthesis, namely water and energy exchanges, analytical solutions of this highly nonlinear system have been provided through optimization assumptions. Despite the appeal of finding analytical solutions of plant photosynthesis processes [*Baldocchi*, 1994; *Lloyd et al.*, 1995; *De Pury and Faruhar*, 1997; *Baldocchi and Amthor*, 2001], this study suggests that optimality

assumptions might be too simplistic leading to undesirable sensitivity confined to few parameters.

4.3. Sensitivity to Soil Moisture

[55] According to our extensive analysis, both with (section 3.2.1) and without (section 3.2.2) photosynthesis-related parameters, the model has a very low sensitivity, in relation to the vegetation outcomes (e.g., biomass, NPP, and LAI), to parameters controlling the terrestrial water balance (Figure 13). This contradicts empirical evidence that emphasizes the effect of water availability on primary production [e.g., *Beer et al.*, 2010; *Reichstein et al.*, 2007]. While it is true that Swiss climate is rather wet, the lack of sensitivity to values of SSC, which directly defines the available water to plants, is also evident in the dry alpine climate regime of Sion, where water controls have shown to be important [*Zweifel et al.*, 2007].

[56] The lack of sensitivity to water is likely ascribed to both an inaccurate representation of water stress effects on vegetation functioning (photosynthesis, autotrophic respiration, and carbon allocation) that are still not fully understood [*Tezara et al.*, 1999; *Tuzet et al.*, 2003; *Zweifel et al.*, 2006; *Vico and Porporato*, 2008; *Lawlor and Tezara*, 2009; *Keenan et al.*, 2010; *McDowell*, 2011; *Tardieu et al.*, 2011] and the simplistic approach used by LPJ-GUESS and several other DGVMs in representing soil hydrology [*Pitman*, 2003; *Jung et al.*, 2007b]. Specifically, the "bucket
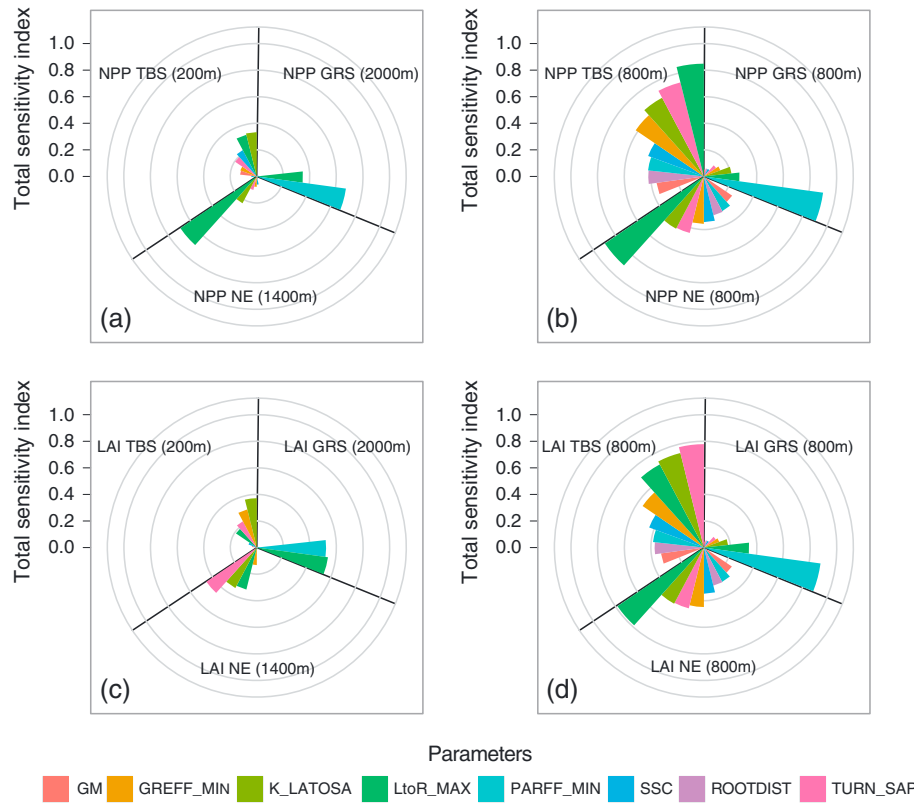
Figure 12. Coxcomb plots of the total effect sensitivity indices for (a and b) NPP and (c and d) LAI. Total effect sensitivity indices of NPP and LAI are reported for the three different elevation bands where each of the simulated PFT is the dominant (TBS at 200 m asl, NE at 1400 m asl, and GRS at 2000 m asl) under normal precipitation conditions (in Figures 12a and 11c), and for the elevation band of 800 m asl where all the PFTs coexist (in Figures 12b and 12d)
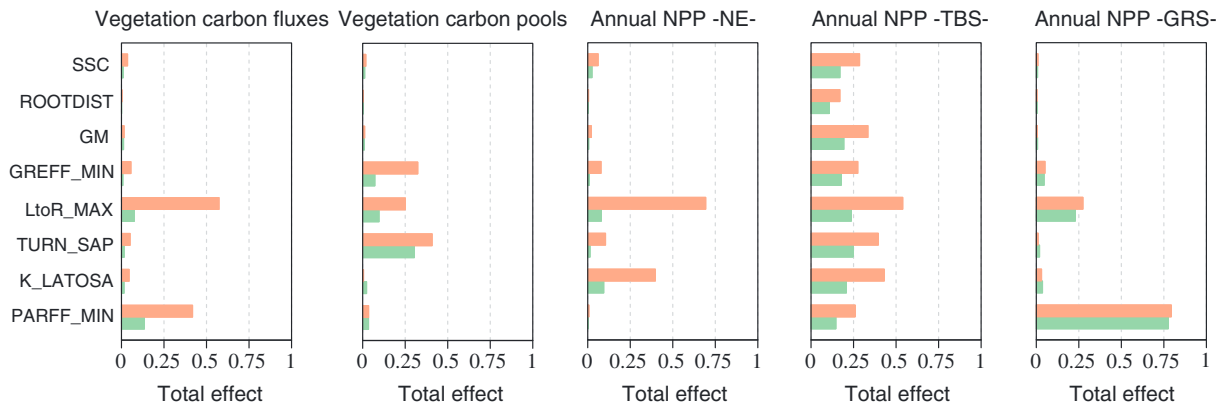
Figure 13. Total-order sensitivity index of the subset of eight examined parameters with the different GSA experiments, including (photosynthesis-on, green bars) and excluding (photosynthesis-off orange bars) parameters related to the Farquhar photosynthesis parameterization (*ALPHA _ C*3, *ALPHA _ A*, and *THETA*). The median of Sobol' total-order sensitivity indices over the 15 examined climatic forcings is plotted.

model" assumption which is implemented in LPJ-GUESS (and in many other DGVMs) [*Haxeltine and Prentice*, 1996a; *Neilson*, 1995; *Gerten et al.*, 2004] might lead to unreliable model results, especially for the case of dry climates, reducing the importance of water limitations [*Churkina et al.*, 1999; *Gordon et al.*, 2004; *Matthews et al.*, 2007; *Morales et al.*, 2007; *Jung et al.*, 2007a; *Dietze et al.*, 2011; *Wood et al.*, 2011]. More detailed approaches

for computing surface and soil water dynamics in an ecohydrological framework [e.g., *Ivanov et al.*, 2008a; *Hwang et al.*, 2009; *Fatichi et al.*, 2012a] or at the tree scale [e.g., *Bohrer et al.*, 2005; *Janott et al.*, 2010; *Bittner et al.*, 2012] might improve the simulation of carbon and water fluxes especially in arid and semiarid regimes [*Hanan et al.*, 1998; *Law et al.*, 2000; *Baldocchi and Wilson*, 2001; *Ivanov et al.*, 2008b; *Quillet et al.*, 2010; *Fatichi et al.*, 2012b]. In these ecosystems, DGVMs are prone to a poorer performance when compared to temperature-limited northern ecosystems [*Smith et al.*, 2001; *Hickler et al.*, 2004; *Morales et al.*, 2005, 2007; *Jung et al.*, 2007a; *Keenan et al.*, 2011b], illustrating that moisture availability is not a primary driver of their performance [*Churkina et al.*, 1999; *Matthews et al.*, 2007].

[57] A more mechanistic representation of plant-water relationships should be thus embedded in the current model framework of DGVMs. This implies not only a better coupling of the intertwined dynamics of photosynthesis, stomatal regulation, and transpiration but also an explicit modeling of water controls on biochemical process, carbon transport, and plant growth as well as a better representation of the driving force, i.e., soil moisture temporal and spatial variability.

4.4. Sensitivity to Stand Composition

[58] The role of stand composition in assessing model sensitivity was demonstrated to be of noticeable importance. The importance of certain parameters with regard to PFT specific outputs is different when compared to the overall parameter sensitivity for the entire stand, highlighting that parameter importance can be strongly affected by the composition of the simulated stand [*Wramneby et al.*, 2008]. Especially, parameters controlling the capability of vegetation biomes to establish and grow become very critical when multiple PFTs compete for the same resources and might undergo stress. As the number of coexisting PFTs in a patch increases, the interactions among parameters also increase leading to a highly susceptible nonlinear system where small variations in the model parameterization may cause considerable differences in the final vegetation composition.

[59] The broad-leaved trees are found more sensitive to different parameterizations, in comparison to needle-leaved trees. This is probably attributed to a different phenology of deciduous PFTs and partially explain the fact that DGVMs are able to simulate evergreen phenology (LAI cycle) and interannual productivity better than the phenology of deciduous trees which is characterized by a strong seasonal variability [*Morales et al.*, 2005; *Kucharik et al.*, 2006; *Jung et al.*, 2007a; *Richardson et al.*, 2011].

[60] The increasing sensitivity to parameterization as a result of a more heterogenous forest highlights another important challenge for DGVMs. Since the simulated species competition is strongly dependent on the choice of the parameters, the robustness of future projections of carbon fluxes might be questionable, especially for conditions different from the ones where parameter values are estimated.

5. Conclusions

[61] Global sensitivity analysis is a very powerful tool for pinpointing principal mechanisms of model functioning and

for highlighting critical aspects of model parameterization and structure. Using this framework, we could show that vegetation carbon fluxes and pools simulated by LPJ-GUESS are highly sensitive to parameters related to photosynthesis, especially to intrinsic quantum efficiency. At the same time, the sensitivity to parameters controlling water availability was found to be very low. Both of these results tend to be in contradiction with recent evidence showing that photosynthesis is not the primary driver of growth while plant-water relations are fundamental. We therefore argue that future amendments of DGVMs should concentrate on a more mechanistic representation of plant-water relations and carbon translocation and allocation, moving away from a photosynthesis (source) centered view of plant growth [*Sala et al.*, 2012]. This, together with an adequate parameterization of plant functional traits, will allow for a better understanding of the terrestrial carbon cycle.

References

Alton, P. B., L. Mercado, and P. North (2007), A sensitivity analysis of the land-surface scheme JULES conducted for three forest biomes: Biophysical parameters, model processes, and meteorological driving data, *Global Biogeochem. Cycles*, 20(GB1008), 1–11, doi:10.1029/2005GB002653.

Anderson, R. G., et al. (2011), Biophysical considerations in forestry for climate protection, *Front. Ecol. Environ.*, 9(3), 174–182, doi:10.1890/090179.

Archer, G., A. Saltelli, and I. Sobol' (1997), Sensitivity measures, ANOVA-like techniques and the use of bootstrap, *J. Stat. Computat. Simul.*, 58(2), 99–120.

Arneth, A., et al. (2010), Terrestrial biogeochemical feedbacks in the climate system, *Nat. Geosci.*, 3(8), 525–532, doi:10.1038/ngeo905.

Bachelet, D., R. Neilson, T. Hickler, R. Drapek, J. Lenihan, M. T. Sykes, B. Smith, S. Sitch, and K. Thonicke (2003), Simulating past and future dynamics of natural ecosystems in the United States, *Global Biogeochem. Cycles*, 17(2), 1045, doi:10.1029/2001GB001508.

Badeck, F., et al. (2001), Tree species composition in European pristine forests: comparison of stand data to model predictions, *Clim. Chang.*, 51(3), 307–347, doi:10.1023/A:1012577612155.

Baldocchi, D. (1994), An analytical solution for coupled leaf photosynthesis and stomatal conductance models, *Tree Physiol.*, 14(7-8-9), 1069–1079, doi:10.1093/treephys/14.7-8-9.1069.

Baldocchi, D., et al. (2001), FLUXNET: A new tool to study the temporal and spatial variability of ecosystem–scale carbon dioxide, water vapor, and energy flux densities, *Bull. Am. Meteorol. Soc.*, 82(11), 2415–2434, doi:10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2.

Baldocchi, D. D. (2008), 'Breathing' of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems, *Aust. J. Bot.*, 56(1), 1–26, doi:10.1071/BT07151.

Baldocchi, D. D., and J. S. Amthor (2001), Canopy photosynthesis: history, measurements and models. In "Terrestrial Global Productivity" (J. Roy, B. Saugier, and H.A. Mooney, Eds.), pp. 9–31. Academic Press, San Diego.

Baldocchi, D. D., and K. B. Wilson (2001), Modeling CO_2 and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales, *Ecol. Model.*, 142(1-2), 155–184, doi:10.1016/S0304-3800(01)00287-3.

Baldocchi, D. D., K. B. Wilson, and L. Gu (2002), How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest-an assessment with the biophysical model CANOAK, *Tree Physiol.*, *22*(15-16), 1065–1077, doi:10.1093/treephys/22.15-16.1065.

Bartelink, H. H. (1998), A model of dry matter partitioning in trees, *Tree Physiol.*, *18*(2), 91–101, doi:10.1093/treephys/18.2.91.

Beer, C., M. Reichstein, E. Tomelleri, P. Ciais, and M. Jung (2010), Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate, *Science*, *329*(5993), 834–838, doi:10.1126/science.1184984.

Beven, K. J. (2006), A manifesto for the equifinality thesis, *J. Hydrol.*, *320*(1-2), 18–36, doi:10.1016/j.jhydrol.2005.07.007.

Bittner, S., N. Legner, F. Beese, and E. Priesack (2012), Individual tree branch-level simulation of light attenuation and water flow of three F. sylvatica L. trees, *J. Geophys. Res.*, *117*(G1), doi:10.1029/2011JG001780.

Bohrer, G., H. Mourad, T. A. Laursen, D. Drewry, R. Avissar, D. Poggi, R. Oren, and G. G. Katul (2005), Finite element tree crown hydrodynamics model (FETCH) using porous media flow within branching elements: A new representation of tree hydrodynamics, *Water Resour. Res.*, *41*(11), 1–17, doi:10.1029/2005WR004181.

Bonan, G. (2008a), Ecological Climatology: Concepts and Applications, Cambridge University Press, Cambridge.

Bonan, G. B. (2008b), Forests and climate change: Forcings, feedbacks, and the climate benefits of forests, *Science*, *320*(5882), 1444–1449, doi:10.1126/science.1155121.

Bonan, G. B., D. Pollard, and L. Thompson (1992), Effects of boreal forest vegetation on global climate, *Nature*, *359*(6397), 716–718, doi:10.1038/359716a0.

Bonan, G. B., S. Levis, L. Kergoat, and K. W. Oleson (2002), Landscapes as patches of plant functional types: An integrating concept for climate and ecosystem models, *Global Biogeochem. Cycles*, *16*(2), doi:10.1029/2000GB001360.

Bonan, G. B., P. J. Lawrence, K. W. Oleson, S. Levis, M. Jung, M. Reichstein, D. M. Lawrence, and S. C. Swenson (2011), Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data, *J. Geophys. Res.*, *116*(G02014), 1–22, doi:10.1029/2010JG001593.

Campolongo, F., and R. Braddock (1999), The use of graph theory in the sensitivity analysis of the model output: A second order screening method, *Reliab. Eng. Syst. Saf.*, *64*(1), 1–12, doi:10.1016/S0951-8320(98)00008-8.

Campolongo, F., J. Cariboni, and A. Saltelli (2007), An effective screening design for sensitivity analysis of large models, *Environ. Model. Software*, *22*(10), 1509–1518, doi:10.1016/j.envsoft.2006.10.004.

Cannell, M., and J. Thornley (1998), Temperature and CO_2 responses of leaf and canopy photosynthesis: A clarification using the non-rectangular hyperbola model of photosynthesis, *Ann. Bot.*, *82*(6), 883–892, doi:10.1006/anbo.1998.0777.

Cariboni, J., D. Gatelli, R. Liska, and A. Saltelli (2007), The role of sensitivity analysis in ecological modelling, *Ecol. Model.*, *203*(1-2), 167–182, doi:10.1016/j.ecolmodel.2005.10.045.

Chan, K., A. Saltelli, and S. Tarantola (1997), Sensitivity analysis of model output: variance-based methods make the difference, in Proceedings of the 29th conference on Winter simulation, pp. 261–268, IEEE Computer Society, Atlanta, Georgia, USA.

Chan, K., A. Saltelli, and S. Tarantola (2000), Winding stairs: A sampling tool to compute sensitivity indices, *Stat. Comput.*, *10*(3), 187–196, doi:10.1023/A:1008950625967.

Chen, H., R. E. Dickinson, Y. Dai, and L. Zhou (2011), Sensitivity of simulated terrestrial carbon assimilation and canopy transpiration to different stomatal conductance and carbon assimilation schemes, *Clim. Dyn.*, *36*(5), 1037–1054, doi:10.1007/s00382-010-0741-2.

Chen, W., R. Jin, and A. Sudjianto (2005), Analytical variance-based global sensitivity analysis in simulation-based design under uncertainty, *J. Mech. Des.*, *127*(5), 875–886, doi:10.1115/1.1904642.

Churkina, G., S. W. Running, A. Schloss, and The Participants Of The Potsdam NPP Model Intercomparison (1999), Comparing global models of terrestrial net primary productivity (NPP): The importance of water availability, *Glob. Chang. Biol.*, *5*(S1), 46–55, doi:10.1046/j.1365-2486.1999.00006.x.

Collatz, G., J. Berry, G. Farquhar, and J. Pierce (1990), The relationship between the Rubisco reaction mechanism and models of photosynthesis, *Plant Cell Environ.*, *13*(3), 219–225, doi:10.1111/j.1365-3040.1990.tb01306.x.

Collatz, G., J. Ball, C. Grivet, and J. Berry (1991), Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer, *Agr. Forest. Meteorol.*, *54*(2-4), 107–136, doi:10.1016/0168-1923(91)90002-8.

Collatz, G., M. Ribas-Carbo, and J. A. Berry (1992), Coupled photosynthesis-stomatal conductance model for leaves of C_4 plants, *Funct. Plant Biol.*, *19*(5), 519–538, doi:10.1071/PP9920519.

Cox, G., J. Gibbons, A. Wood, J. Craigon, S. Ramsden, and N. Crout (2006), Towards the systematic simplification of mechanistic models, *Ecol. Model.*, *198*(1-2), 240–246, doi:10.1016/j.ecolmodel.2006.04.016.

Cox, P., R. Betts, C. Jones, and S. Spall (2000), Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature*, *408*(6809), 184–187, doi:10.1038/35041539.

Cramer, W., D. Kicklighter, A. Bondeau, B. Iii, G. Churkina, B. Nemry, A. Ruimy, A. Schloss, and The Participants Of The Potsdam NPP Model Intercomparison (1999), Comparing global models of terrestrial net primary productivity (NPP): Overview and key results, *Glob. Chang. Biol.*, *5*(S1), 1–15, doi:10.1046/j.1365-2486.1999.00009.x.

Cramer, W., et al. (2001), Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models, *Glob. Chang. Biol.*, *7*(4), 357–373, doi:10.1046/j.1365-2486.2001.00383.x.

Dai, Y., R. Dickinson, and Y. Wang (2004), A two-big-leaf model for canopy temperature, photosynthesis, and stomatal conductance, *J. Climate*, *17*, 2281–2299.

Daudet, F., A. Lacointe, J. Gaudillère, and P. Cruiziat (2002), Generalized Münch coupling between sugar and water fluxes for modelling carbon allocation as affected by water status, *J. Theor. Biol.*, *214*(3), 481–98, doi:10.1006/jtbi.2001.2473.

De Pury, D. G. G., and G. D. Faruhar (1997), Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models, *Plant Cell Environ.*, *20*(5), 537–557, doi:10.1111/j.1365-3040.1997.00094.x.

De Schepper, V., and K. Steppe (2011), Tree girdling responses simulated by a water and carbon transport model, *Ann. Bot.*, *108*(6), 1147–1154, doi:10.1093/aob/mcr068.

Dietze, M. C., et al. (2011), Characterizing the performance of ecosystem models across time scales: A spectral analysis of the North American Carbon Program site-level synthesis, *J. Geophys. Res.*, *116*(G04029), doi:10.1029/2011JG001661.

EC (2009), Impact assessment guidelines, *Tech. Rep. 92*, SEC.

EPA (2009), Guidance on the development, evaluation, and application of environmental models, *Tech. Rep. EPA/100/K-09/003*, Office of the Science Advisor, Council for Regulatory Environmental Modeling.

Evans, M. R. (2012), Modelling ecological systems in a changing world, *Philos. Trans. R. Soc. B: Biol. Sci.*, *367*(1586), 181–190, doi:10.1098/rstb.2011.0172.

Evans, M. R., K. Norris, and T. Benton (2012), Predictive ecology: Systems approaches, *Philos. Trans. R. Soc. B: Biol. Sci.*, *367*(1586), 163–169, doi:10.1098/rstb.2011.0191.

Farquhar, G., S. von Caemmerer, and J. Berry (1980), A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species, *Planta*, *149*(1), 78–90, doi:10.1007/BF00386231.

Fatichi, S., V. Y. Ivanov, and E. Caporali (2012a), A mechanistic ecohydrological model to investigate complex interactions in cold and warm water-controlled environments. 1. Theoretical framework and plot-scale, *J. Adv. Model. Earth Syst.*, *4*(M05002), doi:0.1029/2011MS000086.

Fatichi, S., V. Y. Ivanov, and E. Caporali (2012b), A mechanistic ecohydrological model to investigate complex interactions in cold and warm water-controlled environments. 2. Spatiotemporal analyses, *J. Adv. Model. Earth Syst.*, *4*(M05003), doi:10.1029/2011MS000087.

Fisher, R., N. McDowell, D. Purves, P. Moorcroft, S. Sitch, P. Cox, C. Huntingford, P. Meir, and F. Ian Woodward (2010), Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations, *New Phytol.*, *187*(3), 666–681, doi:10.1111/j.1469-8137.2010.03340.x.

Foley, J. (1994), Net primary productivity in the terrestrial biosphere: The application of a global model, *J. Geophys. Res.*, *99*(D10), 20,773–20,783, doi:10.1029/94JD01832.

Foley, J. (1995), An equilibrium model of the terrestrial carbon budget, *Tellus B*, *47*(3), 310–319, doi:10.1034/j.1600-0889.47.issue3.3.x.

Frank, D. C., J. Esper, C. C. Raible, U. Büntgen, V. Trouet, B. Stocker, and F. Joos (2010), Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate, *Nature*, *463*(7280), 527–530, doi:10.1038/nature08769.

Franklin, O., J. Johansson, R. C. Dewar, U. Dieckmann, R. E. McMurtrie, A. Brännström, and R. Dybzinski (2012), Modeling carbon allocation in trees: A search for principles, *Tree Physiol.*, *32*(6), 648–66, doi:10.1093/treephys/tpr138.

Frayer, W., and G. Furnival (1999), Forest survey sampling designs – A history, *J. Forest.*, *12*(1), 4–10.

Frey, C., and S. Patil (2002), Identification and review of sensitivity analysis methods, *Risk Anal.*, *22*(3), 553–578, doi:10.1111/0272-4332.00039.

Friedlingstein, P., et al. (2006), Climate-carbon cycle feedback analysis: Results from the C^4MIP model intercomparison, *J. Climate*, *19*(14), 3337–3353, doi:10.1175/JCLI3800.1.

Fulton, M. (1991), Adult recruitment as a function of juvenile growth rate in size-structured plant populations, *Oikos*, *62*(1), 102–105.

Gates, D. (2003), Biophysical Ecology, Biology and Medicine Series, Dover Publications, New York.

Gerten, D., S. Schaphoff, U. Haberlandt, W. Lucht, and S. Sitch (2004), Terrestrial vegetation and water balance-hydrological evaluation of a dynamic global vegetation model, *J. Hydrol.*, *286*(1-4), 249–270, doi:10.1016/j.jhydrol.2003.09.029.

Gordon, W., J. Famiglietti, N. Fowler, T. G. F. Kittel, and K. A. Hibbard (2004), Validation of simulated runoff from six terrestrial ecosystem models: Results from VEMAP, *Ecol. Appl.*, *14*(2), 527–545, doi:10.1890/02-5287.

Haddeland, I., et al. (2011), Multi-model estimate of the global terrestrial water balance: Setup and first results, *J. Hydrometeorology*, *12*(5), 869–884, doi:10.1175/2011JHM1324.1.

Hallgren, W., and A. Pitman (2000), The uncertainty in simulations by a Global Biome Model (BIOME3) to alternative parameter values, *Glob. Chang. Biol.*, *6*(5), 483–495, doi:10.1046/j.1365-2486.2000.00325.x.

Hamby, D. (1994), A review of techniques for parameter sensitivity analysis of environmental models, *Environ. Monit. Assess.*, *32*(2), 135–154, doi:10.1007/BF00547132.

Hanan, N., P. Kabat, A. Dolman, and J. Elbers (1998), Photosynthesis and carbon balance of a Sahelian fallow savanna, *Glob. Chang. Biol.*, *4*(5), 523–538, doi:10.1046/j.1365-2486.1998.t01-1-00126.x.

Harcombe, P. (1987), Tree life tables, *Bioscience*, *37*, 557–568.

Hardiman, B., G. Bohrer, C. Gough, C. Vogel, and P. Curtis (2011), The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest, *Ecology*, *92*(9), 1818–1827, doi:10.1890/10-2192.1.

Haxeltine, A., and I. Prentice (1996a), BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, *Global Biogeochem. Cycles*, *10*(4), 693–709, doi:10.1029/96GB02344.

Haxeltine, A., and I. Prentice (1996b), A general model for the light-use efficiency of primary production, *Funct. Ecol.*, *10*(5), 551–561.

Haxeltine, A., I. Prentice, and I. Creswell (1996), A coupled carbon and water flux model to predict vegetation structure, *J. Veg. Sci.*, *7*(5), 651–666.

Heimann, M., and M. Reichstein (2008), Terrestrial ecosystem carbon dynamics and climate feedbacks, *Nature*, *451*(7176), 289–292, doi:10.1038/nature06591.

Hély, C., L. Bremond, S. Alleaume, B. Smith, M. Sykes, and J. Guiot (2006), Sensitivity of African biomes to changes in the precipitation regime, *Glob. Ecol. Biogeogr.*, *15*(3), 258–270, doi:10.1111/j.1466-822x.2006.00235.x.

Hickler, T., B. Smith, M. T. Sykes, M. Davis, S. Sugita, and K. Walker (2004), Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA, *Ecology*, *85*(2), 519–530, doi:10.1890/02-0344.

Hickler, T., et al. (2012), Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model, *Glob. Ecol. Biogeogr.*, *21*(1), 50–63, doi:10.1111/j.1466-8238.2010.00613.x.

Hoch, G., and C. Körner (2012), Global patterns of mobile carbon stores in trees at the high-elevation tree line, *Glob. Ecol. Biogeogr.*, *21*(8), 861–871, doi:10.1111/j.1466-8238.2011.00731.x.

Homma, T., and A. Saltelli (1996), Importance measures in global sensitivity analysis of nonlinear models, *Reliab. Eng. Syst. Saf.*, *52*(1), 1–17, doi:10.1016/0951-8320(96)00002-6.

House, J. I., I. Prentice, N. Ramankutty, R. A. Houghton, and M. Heimann (2003), Reconciling apparent inconsistencies in estimates of terrestrial CO_2 sources and sinks, *Tellus B*, *55*(2), 345–363, doi:10.1034/j.1600-0889.2003.00037.x.

Huang, S., S. J. Titus, and D. P. Wiens (1992), Comparison of nonlinear height-diameter functions for major Alberta tree species, *Can. J. For. Res.*, *22*(9), 1297–1304, doi:10.1139/x92-172.

Hurtt, G. C., P. R. Moorcroft, S. W. Pacala, and S. A. Levin (1998), Terrestrial models and global change: Challenges for the future, *Glob. Chang. Biol.*, *4*(5), 581–590, doi:10.1046/j.1365-2486.1998.t01-1-00203.x.

Hwang, T., L. Band, and T. C. Hales (2009), Ecosystem processes at the watershed scale: Extending optimality theory from plot to catchment, *Water Resour. Res.*, *45*(11), doi:10.1029/2009WR007775.

Ishii, H., and S. Asano (2010), The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests, *Ecol. Res.*, *25*(4), 715–722, doi:10.1007/s11284-009-0668-4.

Ito, A., and T. Sasai (2006), A comparison of simulation results from two terrestrial carbon cycle models using three climate data sets, *Tellus B*, *58*(5), 513–522, doi:10.1111/j.1600-0889.2006.00208.x.

Ivanov, V. Y., R. L. Bras, and E. R. Vivoni (2008a), Vegetation-hydrology dynamics in complex terrain of semiarid areas: 1. A mechanistic approach to modeling dynamic feedbacks, *Water Resour. Res.*, *44*(W03429), doi:10.1029/2006WR005588.

Ivanov, V. Y., R. L. Bras, and E. R. Vivoni (2008b), Vegetation-hydrology dynamics in complex terrain of semiarid areas: 2. Energy-water controls of vegetation spatiotemporal dynamics and topographic niches of favorability, *Water Resour. Res.*, *44*(W03430), doi:10.1029/2006WR005595.

Jackson, R., J. Canadell, J. Ehleringer, H. Mooney, O. E. Sala, and E. D. Schulze (1996), A global analysis of root distributions for terrestrial biomes, *Oecologia*, *108*(3), 389–411, doi:10.1007/BF00333714.

Jakeman, A., R. Letcher, and J. Norton (2006), Ten iterative steps in development and evaluation of environmental models, *Environ. Model. Software*, *21*(5), 602–614, doi:10.1016/j.envsoft.2006.01.004.

Janott, M., S. Gayler, A. Gessler, M. Javaux, C. Klier, and E. Priesack (2010), A one-dimensional model of water flow in soil-plant systems based on plant architecture, *Plant Soil*, *341*(1-2), 233–256, doi:10.1007/s11104-010-0639-0.

Jarvis, P. G. (1995), Scaling processes and problems, *Plant Cell Environ.*, *18*(10), 1079–1089, doi:10.1111/j.1365-3040.1995.tb00620.x.

Jenkinson, D., S. Andrew, J. Lynch, M. Goss, and P. Tinker (1990), The turnover of organic carbon and nitrogen in soil [and discussion], *Philos. Trans. R. Soc. B: Biol. Sci.*, *329*(1255), 361–368, doi:10.1098/rstb.1990.0177.

Jung, M., G. Le Maire, S. Zaehle, S. Luyssaert, M. Vetter, G. Churkina, P. Ciais, N. Viovy, and M. Reichstein (2007a), Assessing the ability of three land ecosystem models to simulate gross carbon uptake of forests from boreal to Mediterranean climate in Europe, *Biogeosciences*, *4*(4), 647–656, doi:10.5194/bg-4-647-2007.

Jung, M., et al. (2007b), Uncertainties of modeling gross primary productivity over Europe: A systematic study on the effects of using different drivers and terrestrial biosphere models, *Global Biogeochem. Cycles*, *21*(GB4021), 1–12, doi:10.1029/2006GB002915.

Keeling, C., S. C. Piper, A. F. Bollenbacher, and J. S. Walker (2009), Atmospheric CO_2 records from sites in the sio air sampling network, *Tech. Rep.*, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A., doi:10.3334/CDIAC/atg.035.

Keenan, T., S. Sabate, and C. Gracia (2010), Soil water stress and coupled photosynthesis conductance models: Bridging the gap between conflicting reports on the relative roles of stomatal, mesophyll conductance and biochemical limitations to photosynthesis, *Agr. Forest. Meteorol.*, *150*(3), 443–453, doi:10.1016/j.agrformet.2010.01.008.

Keenan, T., M. S. Carbone, M. Reichstein, and A. D. Richardson (2011a), The model-data fusion pitfall: Assuming certainty in an uncertain world, *Oecologia*, *167*(3), 587–97, doi:10.1007/s00442-011-2106-x.

Keenan, T., J. M. Serra, F. Lloret, M. Ninyerola, and S. Sabate (2011b), Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO_2 matters!, *Glob. Chang. Biol.*, *17*(1), 565–579, doi:10.1111/j.1365-2486.2010.02254.x.

Keenan, T., et al. (2012), Terrestrial biosphere model performance for interannual variability of land-atmosphere CO_2 exchange, *Glob. Chang. Biol.*, *18*(6), 1971–1987, doi:10.1111/j.1365-2486.2012.02678.x.

Kergoat, L. (1998), A model for hydrological equilibrium of leaf area index on a global scale, *J. Hydrol.*, *212-213*(0), 268–286, doi:10.1016/S0022-1694(98)00211-X.

Kerr, J. T., and M. Ostrovsky (2003), From space to species: Ecological applications for remote sensing, *Trends Ecol. Evol.*, *18*(6), 299–305, doi:10.1016/S0169-5347(03)00071-5.

Kimmins, J., J. Blanco, B. Seely, C. Welham, and K. Scoullar (2008), Complexity in modelling forest ecosystems: How much is enough?, *For. Ecol. Manage.*, *256*(10), 1646–1658, doi:10.1016/j.foreco.2008.03.011.

Knorr, W. (2000), Annual and interannual CO_2 exchanges of the terrestrial biosphere: Process based simulations and uncertainties, *Glob. Ecol. Biogeogr.*, *9*(3), 225–252, doi:10.1046/j.1365-2699.2000.00159.x.

Kobayashi, H., D. D. Baldocchi, Y. Ryu, Q. Chen, S. Ma, J. L. Osuna, and S. L. Ustin (2012), Modeling energy and carbon fluxes in a heterogeneous oak woodland: A three-dimensional approach, *Agr. Forest. Meteorol.*, *152*, 83–100, doi:10.1016/j.agrformet.2011.09.008.

Koca, D., B. Smith, and M. T. Sykes (2006), Modelling regional climate change effects on potential natural ecosystems in Sweden, *Clim. Chang.*, *78*(2), 381–406, doi:10.1007/s10584-005-9030-1.

Körner, C. (2003), Carbon limitation in trees, *J. Ecol.*, *91*(1), 4–17, doi:10.1046/j.1365-2745.2003.00742.x.

Körner, C. (2012), Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits, Springer, Basel.

Krinner, G., N. Viovy, N. de Noblet-Ducoudré, J. Ogée, J. Polcher, P. Friedlingstein, P. Ciais, S. Sitch, and I. Prentice (2005), A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, *Global Biogeochem. Cycles*, *19*(GB1015), doi:10.1029/2003GB002199.

Kucharik, C. J., J. Foley, C. Delire, V. Fisher, M. Coe, J. Lenters, C. Young-Molling, and N. Ramankutty (2000), Testing the performance of a dynamic global ecosystem model: Water balance, carbon balance, and

vegetation structure, *Global Biogeochem. Cycles*, *14*(3), 795–825, doi:10.1029/1999GB001138.

Kucharik, C. J., C. C. Barford, M. E. Maayar, S. C. Wofsy, R. K. Monson, and D. D. Baldocchi (2006), A multiyear evaluation of a Dynamic Global Vegetation Model at three AmeriFlux forest sites: Vegetation structure, phenology, soil temperature, and CO_2 and H_2O vapor exchange, *Ecol. Model.*, *196*(1-2), 1–31, doi:10.1016/j.ecolmodel.2005.11.031.

Law, B., M. Williams, P. Anthoni, D. D. Baldocchi, and M. H. Unsworth (2000), Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a Pinus ponderosa forest subject to soil water deficit, *Glob. Chang. Biol.*, *6*(6), 613–630, doi:10.1046/j.1365-2486.2000.00339.x.

Lawlor, D. W., and W. Tezara (2009), Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: A critical evaluation of mechanisms and integration of processes, *Ann. Bot.*, *103*(4), 561–79, doi:10.1093/aob/mcn244.

Lawrie, J., and J. Hearne (2007), Reducing model complexity via output sensitivity, *Ecol. Model.*, *207*(2-4), 137–144, doi:10.1016/j.ecolmodel.2007.04.013.

Le Quéré, C., et al. (2009), Trends in the sources and sinks of carbon dioxide, *Nat. Geosci.*, *2*(12), 831–836, doi:10.1038/ngeo689.

Leuzinger, S., C. Manusch, H. Bugmann, and A. Wolf (2013), A sink limited growth model improves biomass estimation along boreal and alpine treelines, *Glob. Ecol. Biogeogr.*, doi:10.1111/geb.12047.

Leverenz, J. W. (1988), The effects of illumination sequence, CO_2 concentration, temperature and acclimation on the convexity of the photosynthetic light response curve, *Physiol. Plant.*, *74*(2), 332–341, doi:10.1111/j.1399-3054.1988.tb00639.x.

Levis, S. (2010), Modeling vegetation and land use in models of the Earth System, *Wiley Interdisc. Rev. Clim. Change*, *1*(6), 840–856, doi:10.1002/wcc.83.

Lischke, H., and T. J. Löffler (2006), Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction, *Ecol. Model.*, *198*(3-4), 341–361, doi:10.1016/j.ecolmodel.2006.05.005.

Litton, C. M., J. W. Raich, and M. G. Ryan (2007), Carbon allocation in forest ecosystems, *Glob. Chang. Biol.*, *13*(10), 2089–2109, doi:10.1111/j.1365-2486.2007.01420.x.

Liu, J., J. M. Chen, J. Cihlar, and W. Park (1997), A process-based boreal ecosystem productivity simulator using remote sensing inputs, *Remote Sens. Environ.*, *62*(2), 158–175.

Lloyd, J., J. Grace, A. Miranda, and P. Meir (1995), A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties, *Plant Cell Env.*, *18*(10), 1129–1145, doi:10.1111/j.1365-3040.1995.tb00624.x.

Luo, Y., et al. (2008), Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones, *Glob. Chang. Biol.*, *14*(9), 1986–1999, doi:10.1111/j.1365-2486.2008.01629.x.

Luyssaert, S., E.-D. Schulze, A. Börner, A. Knohl, D. Hessenmöller, B. E. Law, P. Ciais, and J. Grace (2008), Old-growth forests as global carbon sinks, *Nature*, *455*(7210), 213–215, doi:10.1038/nature07276.

Magnani, F., S. Leonardi, R. Tognetti, J. Grace, and M. Borghetti (1998), Modelling the surface conductance of a broad-leaf canopy: Effects of partial decoupling from the atmosphere, *Plant Cell Env.*, *21*(8), 867–879, doi:10.1046/j.1365-3040.1998.00328.x.

Mäkelä, A. (2012), On guiding principles for carbon allocation in eco-physiological growth models, *Tree Physiol.*, *32*(6), 644–7, doi:10.1093/treephys/tps033.

Manson, S. (2001), Simplifying complexity: A review of complexity theory, *Geoforum*, *32*(3), 405–414, doi:doi:10.1016/S0016-7185(00)00035-X.

Matthews, H. D., M. Eby, T. Ewen, P. Friedlingstein, and B. J. Hawkins (2007), What determines the magnitude of carbon cycle-climate feedbacks?, *Global Biogeochem. Cycles*, *21*(2), 1–12, doi:10.1029/2006GB002733.

McDowell, N. G. (2011), Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality., *Plant Physiol.*, *155*(3), 1051–1059, doi:10.1104/pp.110.170704.

McMahon, S. M., et al. (2011), Improving assessment and modelling of climate change impacts on global terrestrial biodiversity, *Trends Ecol. Evol.*, *26*(5), 249–59, doi:10.1016/j.tree.2011.02.012.

Medlyn, B. E., A. P. Robinson, R. Clement, and R. E. McMurtrie (2005), On the validation of models of forest CO_2 exchange using eddy covariance data: Some perils and pitfalls, *Tree Physiol.*, *25*(7), 839–57, doi:10.1093/treephys/25.7.839.

Medvigy, D., and P. R. Moorcroft (2012), Predicting ecosystem dynamics at regional scales: An evaluation of a terrestrial biosphere model for the forests of northeastern North America, *Philos. Trans. R. Soc. B: Biol. Sci.*, *367*(1586), 222–35, doi:10.1098/rstb.2011.0253.

Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft (2009), Mechanistic scaling of ecosystem function and

dynamics in space and time: Ecosystem demography model version 2, *J. Geophys. Res.*, *114*(G1), 1–21, doi:10.1029/2008JG000812.

Meentemeyer, V. (1978), Macroclimate and lignin control of litter decomposition rates, *Ecology*, *59*(3), 465–472.

Melillo, J., A. McGuire, D. Kicklighter, B. Moore, C. Vorosmarty, and A. Schloss (1993), Global climate change and terrestrial net primary production, *Nature*, *363*, 234–240, doi:10.1038/363234a0.

Melillo, J. M., et al. (2002), Soil warming and carbon-cycle feedbacks to the climate system, *Science*, *298*(5601), 2173–6, doi:10.1126/science.1074153.

Miller, P. A., T. Giesecke, T. Hickler, R. H. W. Bradshaw, B. Smith, H. Seppä, P. J. Valdes, and M. T. Sykes (2008), Exploring climatic and biotic controls on Holocene vegetation change in Fennoscandia, *J. Ecol.*, *96*(2), 247–259, doi:10.1111/j.1365-2745.2007.01342.x.

Monteith, J. (1995), Accommodation between transpiring vegetation and the convective boundary layer, *J. Hydrol.*, *166*(3), 251–263, doi:10.1016/0022-1694(94)05086-D.

Moorcroft, P. (2006), How close are we to a predictive science of the biosphere?, *Trends Ecol. Evol.*, *21*(7), 400–407, doi:10.1016/j.tree.2006.04.009.

Moorcroft, P., G. Hurtt, and S. Pacala (2001), A method for scaling vegetation dynamics: The ecosystem demography model (ED), *Ecological Monographs*, *71*(4), 557–585.

Moorcroft, P. R. (2003), Recent advances in ecosystem-atmosphere interactions: An ecological perspective, *Proceedings of the Royal Society B: Biological sciences*, *270*(1521), 1215–27, doi:10.1098/rspb.2002.2251.

Morales, P., T. Hickler, D. P. Rowell, B. Smith, and M. T. Sykes (2007), Changes in European ecosystem productivity and carbon balance driven by regional climate model output, *Glob. Chang. Biol.*, *13*(1), 108–122, doi:10.1111/j.1365-2486.2006.01289.x.

Morales, P., et al. (2005), Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes, *Glob. Chang. Biol.*, *11*(12), 2211–2233, doi:10.1111/j.1365-2486.2005.01036.x.

Morris, M. (1991), Factorial sampling plans for preliminary computational experiments, *Technometrics*, *33*(2), 161–174, doi:10.2307/1269043.

Muller, B., F. Pantin, M. Génard, O. Turc, S. Freixes, M. Piques, and Y. Gibon (2011), Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs, *J. Exp. Bot.*, *62*(6), 1715–29, doi:10.1093/jxb/erq438.

Myneni, R., et al. (2002), Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data, *Remote Sens. Environ.*, *83*, 214–231.

Neilson, R. (1995), A model for predicting continental-scale vegetation distribution and water balance, *Ecol. Appl.*, *5*(2), 362–385, doi:10.2307/1942028.

Novick, K., R. Oren, P. Stoy, J.-Y. Juang, M. Siqueira, and G. Katul (2009), The relationship between reference canopy conductance and simplified hydraulic architecture, *Adv. Water Resour.*, *32*(6), 809–819, doi:10.1016/j.advwatres.2009.02.004.

Oberhuber, W., I. Swidrak, D. Pirkebner, and A. Gruber (2011), Temporal dynamics of non-structural carbohydrates and xylem growth in Pinus sylvestris exposed to drought, *Can. J. Forest Res.*, *41*, 1590–1597, doi:10.1139/X11-084.

Oreskes, N., K. Shrader-Frechette, and K. Belitz (1994), Verification, validation, and confirmation of numerical models in the earth sciences, *Science*, *263*(5147), 641, doi:10.1126/science.263.5147.641.

Ostle, N. J., et al. (2009), Integrating plant-soil interactions into global carbon cycle models, *J. Ecol.*, *97*(5), 851–863, doi:10.1111/j.1365-2745.2009.01547.x.

Pacala, S., C. Canham, and J. J. Silander (1993), Forest models defined by field measurements. I: The design of a northeastern forest simulator, *Can. J. Forest Res.*, *23*, 1980–1988.

Peng, C. (2000), From static biogeographical model to dynamic global vegetation model: A global perspective on modelling vegetation dynamics, *Ecol. Model.*, *135*(1), 33–54, doi:10.1016/S0304-3800(00)00348-3.

Pitman, A. (2003), The evolution of, and revolution in, land surface schemes designed for climate models, *Int. J. Climatol.*, *23*(5), 479–510, doi:10.1002/joc.893.

Pitman, A., A. Henderson-Sellers, and Z.-L. Yang (1990), Sensitivity of regional climates to localized precipitation in global models, *Nature*, *346*, doi:10.1038/346734a0.

Prentice, I., and H. Helmisaari (1991), Silvics of north European trees: Compilation, comparisons and implications for forest succession modelling, *For. Ecol. Manage.*, *42*(1-2), 79–93, doi:10.1016/0378-1127(91)90066-5.

Prentice, I., W. Cramer, S. Harrison, R. Leemans, R. Monserud, and A. Solomon (1992), A global biome model based on plant physiology and dominance, soil properties and climate, *J. Biogeogr.*, *19*(2), 117–134.

Prentice, I., M. T. Sykes, and W. Cramer (1993), A simulation model for the transient effects of climate change on forest landscapes, *Ecol. Model.*, *65*(1-2), 51–70, doi:10.1016/0304-3800(93)90126-D.

Purves, D., and S. Pacala (2008), Predictive models of forest dynamics, *Science*, *320*(5882), 1452–1453, doi:10.1126/science.1155359.

Quillet, A., C. Peng, and M. Garneau (2010), Toward dynamic global vegetation models for simulating vegetation-climate interactions and feedbacks: Recent developments, limitations, and future challenges, *Environmental Reviews*, *18*(1), 333–353, doi:10.1139/A10-016.

R. Core Team (2012), R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.

Radtke, P. J., T. E. Burk, and P. V. Bolstad (2001), Estimates of the distributions of forest ecosystem model inputs for deciduous forests of eastern North America, *Tree Physiol.*, *21*(8), 505–12.

Read, J., R. Hill, and G. Hope (2010), Contrasting responses to water deficits of Nothofagus species from tropical New Guinea and high latitude temperate forests: Can rainfall regimes constrain latitudinal range?, *J. Biogeogr.*, *37*(10), 1962–1976, doi:10.1111/j.1365-2699.2010.02346.x.

Reichstein, M., et al. (2007), Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: A joint flux tower, remote sensing and modelling analysis, *Glob. Chang. Biol.*, *13*(3), 634–651, doi:10.1111/j.1365-2486.2006.01224.x.

Richardson, A. D., et al. (2011), Terrestrial biosphere models need better representation of vegetation phenology: Results from the North American Carbon Program Site Synthesis, *Glob. Chang. Biol.*, *18*(2), 566–584, doi:10.1111/j.1365-2486.2011.02562.x.

Roxburgh, S., et al. (2004), A critical overview of model estimates of net primary productivity for the Australian continent, *Funct. Plant Biol.*, *31*(11), 1043–1059, doi:10.1071/FP04100.

Sala, A., D. R. Woodruff, and F. C. Meinzer (2012), Carbon dynamics in trees: feast or famine?, *Tree Physiol.*, *32*(6), 764–75, doi:10.1093/treephys/tpr143.

Saltelli, A. (1999), Sensitivity analysis: Could better methods be used?, *J. Geophys. Res.*, *104*(D3), 3789–3793, doi:10.1029/1998JD100042.

Saltelli, A. (2002), Making best use of model evaluations to compute sensitivity indices, *Comput. Phys. Commun.*, *145*(2), 280–297, doi:10.1016/S0010-4655(02)00280-1.

Saltelli, A., and P. Annoni (2010), How to avoid a perfunctory sensitivity analysis, *Environ. Model. Software*, *25*(12), 1508–1517, doi:10.1016/j.envsoft.2010.04.012.

Saltelli, A., and M. Scott (1997), Guest editorial: The role of sensitivity analysis in the corroboration of models and its link to model structural and parametric uncertainty, *Reliab. Eng. Syst. Safe.*, *57*(1), 1–4, doi:10.1016/S0951-8320(97)00022-7.

Saltelli, A., K. Chan, and M. Scott (Eds) (2000), *Sensitivity Analysis, Probability and Statistics* series John Wiley and Sons, Chichester, U. K.

Saltelli, A., S. Tarantola, and F. Campolongo (2000b), Sensitivity analysis as an ingredient of modeling, *Statistical Science*, *15*(4), 377–395, doi:10.1214/ss/1009213004.

Saltelli, A., S. Tarantola, F. Campolongo, and M. Ratto (2004), Sensitivity Analysis in Practice: A Guide to Assessing Scientific Models, Wiley Chichester.

Saltelli, A., M. Ratto, S. Tarantola, and F. Campolongo (2006), Sensitivity analysis practices: Strategies for model-based inference, *Reliab. Eng. Syst. Safe.*, *91*(10-11), 1109–1125, doi:10.1016/j.ress.2005.11.014.

Saltelli, A., M. Ratto, T. Andres, F. Campolongo, J. Cariboni, D. Gatelli, M. Saisana, and S. Tarantola (2008), Global Sensitivity Analysis: The Primer, Wiley-Blackwell, Chichester.

Saltelli, A., P. Annoni, I. Azzini, F. Campolongo, M. Ratto, and S. Tarantola (2010), Variance based sensitivity analysis of model output. Design and estimator for the total sensitivity index, *Comput. Phys. Commun.*, *181*(2), 259–270, doi:10.1016/j.cpc.2009.09.018.

Sato, H., A. Ito, and T. Kohyama (2007), SEIB-DGVM: A new Dynamic Global Vegetation Model using a spatially explicit individual-based approach, *Ecol. Model.*, *200*(3-4), 279–307, doi:10.1016/j.ecolmodel.2006.09.006.

Schwalm, C. R., et al. (2010), A model-data intercomparison of CO_2 exchange across North America: Results from the North American Carbon Program site synthesis, *J. Geophys. Res.*, *115*(G00H05), doi:10.1029/2009JG001229.

Sheng, G., M. Elzas, T. Oren, and B. Cronhjort (1993), Model validation: A systemic and systematic approach, *Reliab. Eng. Syst. Safe.*, *42*(2-3), 247–259, doi:10.1016/0951-8320(93)90092-D.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira (1964), A quantitative analysis of plant form-the pipe model theory: I. Basic analyses, *Jpn. J. Ecol.*, *14*(3), 97–105.

Singsaas, E. L., D. R. Ort, and E. H. DeLucia (2001), Variation in measured values of photosynthetic quantum yield in ecophysiological studies, *Oecologia*, *128*(1), 15–23, doi:10.1007/s004420000624.

Sitch, S., et al. (2003), Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Glob. Chang. Biol.*, *9*(2), 161–185, doi:10.1046/j.1365-2486.2003.00569.x.

Sitch, S., et al. (2008), Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs), *Glob. Chang. Biol.*, *14*(9), 2015–2039, doi:10.1111/j.1365-2486.2008.01626.x.

Smith, B., I. Prentice, and M. T. Sykes (2001), Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space, *Glob. Ecol. Biogeogr.*, *10*(6), 621–637.

Sobol', I. (1967), On the distribution of points in a cube and the approximate evaluation of integrals, *Comput. Math. Math. Phys.*, *7*(4), 86–112.

Sobol', I. (1976), Uniformly distributed sequences with an additional uniform property, *USSR Comput. Math. Math. Phys.*, *16*(5), 236–242, doi:10.1016/0041-5553(76)90154-3.

Sobol', I. (1993), Sensitivity analysis for nonlinear mathematical models, *Math. Model Comput. Exp.*, *1*(4), 407–414.

Stewart, J., and L. Gay (1989), Preliminary modelling of transpiration from the FIFE site in Kansas, *Agr. Forest. Meteorol.*, *48*(3-4), 305–315.

Sugiura, D., and M. Tateno (2011), Optimal leaf-to-root ratio and leaf nitrogen content determined by light and nitrogen availabilities., *PLoS One*, *6*(7), e22,236, doi:10.1371/journal.pone.0022236.

Sumner, D. M., and J. M. Jacobs (2005), Utility of Penman-Monteith, Priestley-Taylor, reference evapotranspiration, and pan evaporation methods to estimate pasture evapotranspiration, *J. Hydrol.*, *308*(1-4), 81–104, doi:10.1016/j.jhydrol.2004.10.023.

Tang, G., and P. J. Bartlein (2008), Simulating the climatic effects on vegetation: Approaches, issues and challenges, *Prog. Phys. Geog.*, *32*(5), 543–556, doi:10.1177/0309133308100443.

Tardieu, F., C. Granier, and B. Muller (2011), Water deficit and growth. Coordinating processes without an orchestrator?, *Curr. Opin. Plant Biol.*, *14*(3), 283–289.

Tezara, W., V. Mitchell, S. Driscoll, and D. Lawlor (1999), Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP, *Nature*, *401*(6756), 914–917, doi:10.1038/44484.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann (1997), The influence of functional diversity and composition on ecosystem processes, *Science*, *277*(5330), 1300–1302, doi:10.1126/science.277.5330.1300.

Tuzet, A., A. Perrier, and R. Leuning (2003), A coupled model of stomatal conductance, photosynthesis and transpiration, *Plant Cell Environ.*, *26*(7), 1097–1116, doi:10.1046/j.1365-3040.2003.01035.x.

Vico, G., and A. Porporato (2008), Modelling C3 and C4 photosynthesis under water-stressed conditions, *Plant Soil*, *313*(1-2), 187–203, doi:10.1007/s11104-008-9691-4.

von Caemmerer, S. (2000), Biochemical models of leaf photosynthesis, Techniques in plant sciences, CSIRO Pub.

Wallach, D., and M. Genard (1998), Effect of uncertainty in input and parameter values on model prediction error, *Ecol. Model.*, *105*(2-3), 337–345, doi:10.1016/S0304-3800(97)00180-4.

Wang, Z., et al. (2011), Evaluating weather effects on interannual variation in net ecosystem productivity of a coastal temperate forest landscape: A model intercomparison, *Ecol. Model.*, *222*(17), 3236–3249, doi:10.1016/j.ecolmodel.2011.06.005.

Waring, R., and P. Schroeder (1982), Application of the pipe model theory to predict canopy leaf area, *Can. J. Forest*, *12*(3), 556–560, doi:10.1139/x82-086.

Weisberg, M. (2007), Who is a modeler?, *Brit. J. Philos. Sci.*, *58*(2), 207–233, doi:10.1093/bjps/axm011.

Whitehead, D., F. Kelliher, C. Frampton, and M. Godfrey (1994), Seasonal development of leaf area in a young, widely spaced *Pinus radiata* D. Don stand, *Tree Physiol.*, *14*(7-8-9), 1019–1038, doi:10.1093/treephys/14.7-8-9.1019.

Wohlfahrt, G., M. Bahn, E. Haubner, I. Horak, W. Michaeler, K. Rottmar, U. Tappeiner, and A. Cernusca (1999), Inter-specific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use, *Plant Cell Environ.*, *22*(10), 1281–1296, doi:10.1046/j.1365-3040.1999.00479.x.

Wolf, A., E. Blyth, R. Harding, D. Jacob, E. Keup-Thiel, H. Goettel, and T. Callaghan (2008), Sensitivity of an ecosystem model to hydrology and temperature, *Clim. Chang.*, *87*(1), 75–89, doi:10.1007/s10584-007-9339-z.

Wolf, A., P. Ciais, V. Bellassen, N. Delbart, C. B. Field, and J. A. Berry (2011), Forest biomass allometry in global land surface models, *Global Biogeochem. Cycles*, *25*(GB3015), 1–16, doi:10.1029/2010GB003917.

Wood, E. F., et al. (2011), Hyperresolution global land surface modeling: Meeting a grand challenge for monitoring Earth's terrestrial water, *Water Resour. Res.*, *47*(5), 1–10, doi:10.1029/2010WR010090.

Wramneby, A., B. Smith, S. Zaehle, and M. T. Sykes (2008), Parameter uncertainties in the modelling of vegetation dynamics – Effects on tree community structure and ecosystem functioning in European forest biomes, *Ecol. Model.*, *216*(3-4), 277–290, doi:10.1016/j.ecolmodel.2008.04.013.

Würth, M. K. R., K. Winter, and C. Körner (1998), Leaf carbohydrate responses to CO_2 enrichment at the top of a tropical forest, *Oecologia*, *116*(1-2), 18–25, doi:10.1007/PL00013821.

Zaehle, S., S. Sitch, B. Smith, and F. Hatterman (2005), Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, *Global Biogeochem. Cycles*, *19*(GB3020), doi:10.1029/2004GB002395.

Zaehle, S., et al. (2007), Projected changes in terrestrial carbon storage in europe under climate and land-use change, 1990–2100, *Ecosystems*, *10*(3), 380–401, doi:10.1007/s10021-007-9028-9.

Zeide, B. (1993), Primary unit of the tree crown, *Ecology*, *74*(5), 1598–1602.

Zweifel, R., F. Zeugin, L. Zimmermann, and D. M. Newbery (2006), Intraannual radial growth and water relations of trees – Implications towards a growth mechanism, *J. Exp. Bot.*, *57*(6), 1445–1459, doi:10.1093/jxb/erj125.

Zweifel, R., K. Steppe, and F. J. Sterck (2007), Stomatal regulation by microclimate and tree water relations: Interpreting ecophysiological field data with a hydraulic plant model, *J. Exp. Bot.*, *58*(8), 2113–2131, doi:10.1093/jxb/erm050.