

Student thesis series INES nr 424

Modelling global Gross Primary Production using the correlation between key leaf traits

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2017
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Alexandra Pongracz (2017).

Modelling global Gross Primary Production using the correlation between key leaf traits
Modellering av global primärproduktion genom att använda korrelation mellan lövens nyckelegenskaper

Bachelor degree thesis, 15 credits in *Physical Geography and Ecosystem Science*
Department of Physical Geography and Ecosystem Science, Lund University

Level: Bachelor of Science (BSc)

Course duration: March 2017 until June 2017

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Modelling global Gross Primary Production using the correlation between key leaf traits

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Bachelor thesis, 15 credits, in *Physical Geography and Ecosystem Science*

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Abstract

Sophisticated ecosystem models make it possible to evaluate the potential future changes of the carbon sequestration capacity of the terrestrial biosphere, as a response to the rapid environmental and climatic changes. Accuracy of model estimates is however strongly dependent on the parametrisation of driving parameters. A previous study of Wang et al. (2012) suggests, that the knowledge of the relationship between key leaf traits may be used to constrain modelled global terrestrial GPP ranges.

Access to extensive leaf trait databases (such as GLOPNET and TRY) open possibilities to develop a more mechanistic rather than empirical based methods of representing vegetation in ecosystem models. Prentice et al. (2015) suggests that a stochastic parametrisation approach should be considered as a future improvement in ecosystem model development.

This thesis discusses the effect of varying key leaf attribute values on derived GPP estimates. Leaf parameters – specifically leaf longevity, leaf nitrogen content and leaf mass per area – are varied within their potential ranges, either individually one-at-a-time or leaf longevity and leaf N traits simultaneously. The methods are applied for LPJ-GUESS DGVM and a simple idealised model (LEIA), that accounts for GPP's dependency on leaf traits.

According to the results, adjusting leaf lifespan values for evergreen and summergreen groups, as well as leaf N yielded a substantial reduction in global annual GPP variance, along with a decrease in mean global estimates. Findings suggest that using the correlation between leaf attributes may significantly improve LPJ-GUESS's performance.

Keywords

ecosystem modelling, leaf longevity, leaf nitrogen content, leaf mass per area, LEIA, LPJ-GUESS, GPP, terrestrial biosphere

Sammanfattning

Avancerade ekosystemmodeller gör det möjligt att undersöka potentiella framtida förändringar i växters förmåga att binda koldioxid via fotosyntes, som en respons till miljö- och klimatförändringar. Precisionen av modellberäkningar är dock starkt beroende av parametrisering av drivande parametrar. En tidigare studie av Wang et al. (2012) föreslår att kunskap om korrelationen mellan lövens nyckelegenskaper kan minska spännvidden av GPP-beräkningar.

Att ha tillgång till utförliga databaser av lövens egenskaper – såsom TRY och GLOPNET – öppnar nya möjligheter för att utveckla mer mekaniska, snarare än empiriska metoder för att representera vegetationen i modeller. Prentice et al. (2015) föreslår att en s.k. stokastisk parametrisation metod skulle kunna användas i den framtida utvecklingsprocessen av ekosystemmodeller.

Denna uppsats diskuterar effekten av varierande egenskaper hos löven, baserat på beräkningar av GPP. Lövegenskaper – speciellt lövens livslängd, lövmassa per område samt lövens kvävekoncentration – är varierade i ett bestämt potentiellt omfång, antingen individuellt eller både med livslängd och kväveinnehåll. Metoderna används i LPJ-GUESS DGVM och en enkel idealiserad modell LEIA, som beräknar GPP beroende på de analyserade lövegenskaperna.

Resultaten antyder att varierande lövegenskaper ger i en signifikant minskning i variationen av de globala årliga GPP beräkningarna, oavsett om variationen i egenskaperna sker individuellt eller genom att beakta livslängd och kväveinnehåll samtidigt.

Undersökningsresultatet visar att kunskap om relationen mellan lövegenskaper kan användas för att begränsa omfånget av GPP beräkningar och följaktligen förbättra LPJ-GUESS:s utförande.

Nyckelord

ekosystemmodellering, lövens livslängd, lövens kvävekoncentration, lövmassa per område, LEIA, LPJ-GUESS, GPP

Acknowledgement

Firstly, I would like to say special thanks to my supervisor Andrew McRobert, for his guidance and support throughout this thesis. His feedbacks and comments are well appreciated and helped a lot to improve this document. I am also thankful to everyone at the Department of Physical Geography and Ecosystem Science who helped me along the way with suggestions and interesting discussions. Last, but not least I would like to thank my parents for their support and patience under this period.

This thesis would not be the same without you!

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1. Introduction

Human-induced changes in the global carbon cycle are unequivocal (IPCC 2014), and largely due to anthropogenic emissions, the atmospheric CO₂ concentration is increasing steadily since the beginning of the industrial era. The emissions of CO₂ and other greenhouse gases (GHGs) contribute to the warming of our climate (IPCC 2014), thus there is an increasing need to assess the potential future changes, in order to be able to implement mitigation and adaptation measures.

Terrestrial ecosystems have an important role in the global carbon cycle, taking up approximately 30% of carbon emissions, thus acting as a countermeasure to anthropogenic emissions (IPCC 2014, Le Quéré et al. 2016). The size of terrestrial carbon sink increased in the period between 2006 and 2015, compared to earlier periods (Le Quéré et al. 2016). It is not clear however if the current land sinks will persist, or how their carbon sequestration capacity will change in the future, as a consequence of changing environmental conditions and rising CO₂ concentrations.

With the aim of evaluating carbon balance patterns Ahlström et al. (2012), used a dynamic global vegetation model (LPJ-GUESS) with climatic input derived from a number of climate models included in the CMIP5 project (Climate Model Intercomparison Project Phase 5). The study found that the terrestrial biosphere turned into a net source of carbon before year 2100 in nearly 60% of the simulations. Besides the large difference in the future projections of ecosystems' carbon storage capacity using different approaches for the estimations, there is also high inter-annual variability in uptake capacity and uncertainty regarding the spatial location of land sinks (Cramer et al. 2001). Currently, several studies are aimed at estimating global CO₂ emissions and the potential sinks, along with decreasing the uncertainty in the model projections (Le Quéré et al. 2016). Using data assimilation techniques or Bayesian fusion, show significant decrease in the land sink size uncertainty (Li et al. 2016).

Having an integral role in the global carbon cycle, terrestrial ecosystems, the related atmosphere-carbon interactions and vegetation dynamics should to be further examined, since they affect the magnitude of land sinks (Cramer et al. 2001).

1.1. Related study

Wang et al. (2012) applied the correlations between three leaf parameters - leaf mass per area, leaf lifespan and leaf nitrogen concentration - using the Australian Community Atmosphere Biosphere Land Exchange model (CABLE). Their results showed that the range of global Gross Primary Production (GPP) estimates decreased, while the mean value of annual estimates did not change significantly (Wang et al. 2012). It is of interest to evaluate the results which can be obtained using a similar method in a model with a different structural set-up.

1.2. Hypothesis

Using the correlation between key leaf traits can reduce the uncertainty (variance) in the modelled global annual GPP estimates.

1.3. Project aim and objectives

The objectives of the two main parts of this study are as follows:

Part 1

- › evaluate how the global GPP estimates of LPJ-GUESS are influenced by the variation of leaf longevity and leaf N content, by analysing the change in the mean and variance of GPP outputs
- › assess how estimates change including and excluding the covariance between lifespan and N content (Correlated and Uncorrelated cases, respectively).

Part 2

- › assign a theoretical annual GPP range, using an 'idealised' model (LEIA), based on empirical relationships that account for GPP's dependency on leaf longevity, leaf mass per area and leaf N content.

A general aim is to test the above-stated hypothesis, interpreting the results acquired from Part 1 and Part 2, to answer the question if the adjustment of leaf parameters can be used as a constraint in ecosystem models.

2. Background

2.1. Global Primary Production

Gross Primary Production is a relevant flux linked to ecosystem carbon balance, that can be defined as the influx of carbon to the ecosystem, the amount of carbon assimilated by vegetation through photosynthesis. Since different indices describing the state of the ecosystem, such as net primary production (NPP) are closely related to GPP, (NPP can be calculated as the difference between GPP and autotrophic respiration) the uncertainty in primary production estimates influences the overall quality of future predictions. Net Primary Production accounts for over 40% of the uncertainty regarding the amount of carbon the biosphere is able to bound (Ahlström et al. 2015).

There are no direct ways to quantify GPP, so different approaches have to be employed as a proxy instead of measurements. To date, a number of methods have been developed to determine the potential range of GPP (Table 1). Annual global gross primary production estimates vary between 100 and 175 Pg C year⁻¹, having a mean of approximately 120 Pg C year⁻¹.

Table 1. Comparison between global annual Gross Primary Production estimates, using different methods, for further description see source literature.

Method	GPP estimate (Pg C yr ⁻¹)	Source
LPJ-GUESS Dynamic Global Vegetation Model	112	Smith et al. (2014)
Remote sensing approach (fPAR)	118 \pm 1	Zhao et al. (2005)
Eddy covariance measurements, upscaling flux observations with a machine learning technique	119 \pm 6	Jung et al. (2012)
Observation based estimates	123 \pm 8	Beer et al. (2010)
BETHY Terrestrial Biosphere Model	163	Kattge et al. (2009)
Stable isotope analysis, (¹⁸ O/ ¹⁶ O and ¹³ C/ ¹² C)	150-175	Welp et al. (2011)

Global carbon budgets account for the size of land sink (difference between GPP and respiration) as the residual of other measured fluxes, also considering estimates of various methods (Le Quéré et al. 2016). For the sake of providing more reliable estimates of forthcoming changes, it is important to evaluate different methods, to decrease the uncertainty associated with GPP outputs and indirectly other ecosystem fluxes.

2.2. Ecosystem modelling

One of the common tools used to assess future environmental conditions are ecosystem models. These models are based on empirical and mechanistic relationships between forcing variables and derived outputs. In process-based models, functions describing complex processes - such as photosynthesis, require the estimation of certain input values. Appointing “best guess” parameter values introduces source of uncertainty in the models’ performance. Other sources include the uncertainty and errors in the driving data, and imperfect process representations. Appropriate parametrisation of leaf phenology in ecosystem models is essential, due to the fact that phenology affects the amount of carbon taken up by the vegetation. Yet it is a challenging task, because of the complex nature of phenological processes and the potential gaps in knowledge in this area (Arora and Boer 2005). Various models adapt a simplified framework to represent different species, through defining so-called Plant Functional Types (PFTs). These groups are characterized by a list of bioclimatic attributes that limit their growth and reproduction, and furthermore define their potential habitats. Reich et al. (2007) points out, that since the variation in plant traits is better described on a continuous scale rather than in discrete groups (for instance as PFTs), an adaptive vegetation classification scheme could yield a representative model presentation of terrestrial vegetation.

Previous published studies have investigated the relationship between different leaf traits and how they affect ecosystem productivity (Reich et al. 1992; Wright et al. 2004). Collectively these studies show, that there is a strong co-dependency between specific leaf area, leaf longevity, leaf nitrogen content and the net photosynthetic rate (Reich et al. 1992; Wright et al. 2004). A deeper understanding on the role of leaf properties can lead to a more comprehensive understanding of ecosystem functioning, and prompt the development of trait representation in ecosystem models.

2.3. Leaf form and function

By adjusting soft leaf attributes, plants apply so-called adaptive trade-offs, to optimize their performance and survival (Monson and Baldocchi 2014). These trade-offs and cost-benefit optimization can yield a common universal pattern in leaf trait affiliation.

Wright et al. (2004) created the Global Plant Trait Network (GLOPNET), that was used to produce a global leaf economics spectrum review. The term leaf economics spectrum refers to the observed pattern and covariation of chemical, physiological and structural leaf traits. In their study, Wright et al. (2004) concluded that the analysed significant trait relationship patterns are consistent globally, without regard to species, spatial extent, biomes or ecosystems.

2.4. Traits in focus

Leaf nitrogen (N_{leaf} , [gN gC⁻¹]) and its relationship on photosynthetic capacity are considered as sensitive parameters in terrestrial biosphere models (Kattge et al. 2009). Nitrogen is identified as a primary control of the photosynthetic rate, influencing the maximum carboxylation capacity. Approximately 35% of leaf N is accounted for within the Rubisco enzyme that has an important role as a catalyst of photosynthesis (Monson and Baldocchi 2014).

Leaf longevity or leaf lifespan (LL, [year]) describes the average time a leaf persists on a plant. Reich et al. (1992) refers to LL as an “ecological integrator”, as it is related closely to other traits. Lifespan varies widely amongst species depending on phenology. Evergreens tend to have longer leaf longevity, and deciduous species shorter lifespan (Reich et al. 1992; Monson and Baldocchi 2014).

Leaf lifespan and leaf N content are strongly related to each other, as confirmed by several studies (Reich et al. 1992; Wright et al. 2004). An increase in LL can be associated a decrease in mass based leaf N content and furthermore a decline in the net photosynthetic rate (Reich et al. 1992).

Leaf mass per area (LMA , [kg m⁻²]) shows the dry-biomass investment in construction of new leaves per unit leaf area (Wright et al. 2004). This trait is positively correlated to leaf longevity and negatively correlated to leaf N content and photosynthetic rate. LMA can be evaluated as a proxy of ecological strategies of plants (Lusk et al. 2008).

Leaf longevity and leaf mass per area influence the modelled canopy area and thus indirectly the photosynthetic rate (Wang et al. 2012).

Specific leaf area (SLA , [m² kg C⁻¹]) is a measure of leaf thickness, and it is the leaf property connecting leaf form and function (Monson and Baldocchi 2014). SLA is positively correlated to the net rate of photosynthesis. The SLA index can be calculated as the inverse of LMA (Lusk et al. 2008), in this study it is used as a proxy for estimating LMA (Part 2, see Eq. 6).

Leaf area index (LAI , [m² m⁻²]) describes the ratio between the leaf area over the occupied ground area. Since LAI defines the canopy area, it can be linked to and affect a number of ecosystem processes (Asner et al. 2003).

In their study Wright et al. (2004) claims that the relationship between the presented leaf traits can be explained by the leaf economic spectrum. This spectrum extends from slow to fast return sections depending the processing rate of investments and nutrients. Species at the slow-end can be characterized by long leaf life span, corresponding high leaf mass per area, and low rates of photosynthesis. The fast-end of the spectrum is featured by species with short leaf lifespan, low LMA and higher photosynthetic rate (Wright et al. 2004). Considering the relationships between leaf

attributes when assigning parameter values for leaf traits might be used to achieve a more process-based, rather than empirical approach and thus, potentially lead to less uncertainty regarding the derived output variables.

3. Methods

The project can be divided in two main parts, which are to be referred to as Part 1 and Part 2 in the following sections. Model specific details are outlined individually for the respective parts in section 3.3 and 3.4, while data processes and analysis are treated on the whole in section 3.5. Representation of the study's workflow can be seen in Figure A1 in the Appendix.

3.1. Data acquisition

Leaf parameter indices were derived from the GLOPNET dataset (Wright et al. 2004), that represents over 2500 species from all major vegetation groups. The range of trait values was determined by the minimum and maximum values for each vegetation group.

Table 2. Leaf nitrogen content and leaf longevity parameter minimum, maximum and mean values based on the GLOPNET dataset (Wright and Reich 2011).

Vegetation classification	N_{leaf} (gN gC ⁻¹) [%]			LL (year)		
	min.	max.	mean	min.	max.	mean
evergreen	0.003617 [0.87]	0.01775 [4.27]	0.00715 [1.72]	0.90	20.00	3.73
tropical evergreen				0.21	24.00	1.90
summergreen				0.13	0.92	0.44

Leaf nitrogen content parameter is set as a constant value of 0.00715 gN gC⁻¹ in LPJ-GUESS, based on Haxeltine and Prentice (1996). Taking this estimate as the mean value and as the equivalent of 1.72% leaf N content – the mean leaf N content calculated from the available records in the GLOPNET database, where N is specified as % -, maximum and minimum mass based N concentrations were calculated. Hence, the range of N_{leaf} in mass units was used as stated in Table 2.

3.2. Realization of trait relationships

Leaf lifespan varies across a potential range between species and vegetation groups, rather than having a constant set value. To simulate natural conditions, two different methods are to be applied. Using the Uncorrelated case, where each trait is varied across their plausible range of values, assuming uniform distribution. As mentioned earlier, the correlation between the specified leaf properties is well studied, therefore another technique is also implemented. This Correlated case looks a step further by accounting for the known covariance between leaf longevity and leaf N, adjusting these parameters simultaneously using a linear function.

3.3. Part 1

For the first part of the project (Part 1) LPJ-GUESS dynamic global vegetation model (DGVM) version 3.1 was employed in global, cohort mode (for detailed description of the model see: Smith et al. (2001), Sitch et al. (2003) and Smith et al. (2014)). LPJ-GUESS is a suitable tool to investigate the terrestrial-atmospheric carbon interactions, because this DGVM accounts for processes such as CO₂ fertilisation, population dynamics (succession and competition) along with N deposition and carbon-nitrogen interactions.

3.3.1. Driving data

Climatic input was specified from the Climate Research Unit (CRU) TS 3.0 dataset with 0.5° resolution for the period 1901-2006; CO₂ concentration data were derived from the NOAA Earth System Research Laboratory Mauna Loa Observatory measurements dataset, and soil data from FAO's Digitized soil map (Mitchell and Jones 2005, FAO 2003). Nitrogen deposition data was acquired from Lamarque et al. (2013) (ACCMIP database). Each simulation was initialised by a 300 year spin up period to determine the base conditions prior to the scenario start.

3.3.2. Vegetation classification

In this project, a standard set of 10 plant functional types (PFTs) were used (see Table A1). Three major vegetation classes - summergreen, evergreen and tropical evergreen (see Table A2) - were defined on the basis of phenology. Leaf longevity parameter values were adjusted individually for these groups, whereas leaf nitrogen content was varied uniformly amongst all PFTs as stated in Table 2. The reason for this approach is that leaf longevity widely varies depending on phenology and adjusting parameter values accordingly, the outputs are assumed to be more realistic (Reich et al. 1992).

Because of time constraints of this project, leaf longevity was not adjusted specifically for C3 and C4 grasses, and these PFTs are not further analysed in this study. Likewise, land-use change and crops are not discussed further.

3.3.3. Simulation protocol

GPP was simulated on 13 sites (gridpoints) with a size of 1000 km², distributed over the globe, representing all climatic conditions. In this project two replicate patches were applied for each site. To test the presented hypothesis, a sensitivity-like analysis was carried out using LPJ-GUESS. The model was run multiple times – 100 and 50 iterations per group for the Uncorrelated and Correlated cases respectively- and the properties of the emergent outputs were analysed. The section below describes the two applied methods' workflow.

3.3.3.1. Uncorrelated case

Simulations were performed in batches for the specific groups, initiated by a script in Matlab. At each simulation one of the four (leaf longevity for evergreens, tropical evergreens and summergreens, as well as leaf N), were selected randomly from the specified range (see Table 2), assuming uniform distribution. The other parameters' values were not changed; the default best guess values were used. Having 100 iterations per parameter, a total of 400 outputs were generated.

3.3.3.2. Correlated case

Leaf N value was assigned using the fitted linear relationship based on the study of Reich et al. (1992) using the following equation:

$$\log(N_{leaf}) = 1.61 - 0.31 \times \log(LL) \quad (1)$$

The value was redrawn in case a lower than potential minimum or higher than potential maximum value had been chosen. Leaf longevity values were chosen randomly from a normal distribution with the mean value corresponding to the specific vegetation group's mean value (based on the GLOPNET dataset as noted in Table 2). In the event negative or higher than potential maximum lifespan values were drawn, the value has been reselected. In total, 150 outputs were generated.

As a validation step of the Correlated case GPP estimates, another set of LPJ-GUESS runs were carried out. LL and leaf N pairs were selected as driving parameters from the GLOPNET database's available complete observational pairs. This step was performed to examine if the emergent outputs' behaviour differ using observational- and the linear function based (Eq.1) LL and leaf N pairs as forcing parameters. Just as the previous case, a total of 150 simulations were performed. The distribution of leaf longevity and leaf N pairs created by the above-mentioned methods can be seen on Figure A2 and A3 in the Appendix.

3.4. Part 2

3.4.1. LEIA: model description

This idealised model can be classified as dynamic, in relation to the changing forcing variables- as temperature and CO₂ input data is specified as a time series. Understanding the underlying processes is not of interest in this case, hence the application of the model is functional. The emergent outputs, (global, annual GPP estimates) are in focus in this study. These attributes show, that the model is deterministic and qualitative as to its outputs. Global primary production is not analysed spatially; the resolution of the model is global and the temporal resolution is 69 years.

Several assumptions were set, for instance forcing variables are defined as global mean values for the sake of simplicity (for an in-depth description of the model see 8.7. in the Appendix). LEIA applies a mechanistic approach of estimating photosynthesis, as the minimum of the two limiting rates- electron transport - and carboxylation rate -, based on the Farquhar model (Haxeltine and Prentice 1996).

GPP dependency on the investigated three leaf traits are accounted for with the help of Eq. 2, where LAI functions as a link between leaf attributes and photosynthetic capacity. For a conceptual representation of the model structure see Figure 1.

$$LAI = Leaf_C^{new} - \frac{(\gamma_{lm} \times LAI_{old} / 366)}{SLD} \quad (2)$$

In Eq. 2 $Leaf_C^{new}$ [kg C m⁻²] represents the fraction of C allocated to the construction of new biomass, γ_{lm} [360 year⁻¹] accounts for leaf mortality (biomass loss), and SLD [kg C / m² m⁻² LAI] denotes specific leaf density for the specified groups, based on Clark et al. (2011).

3.4.2. Driving data

The same CO₂ dataset was used as for Part 1. Monthly air temperature data was collected from the NOAA NCEP/NCAR Reanalysis Monthly Means Database with 2.5° spatial resolution (Saha et al. 2010). As a pre-processing step, monthly means were averaged over a global scale. Leaf area index input for the first simulation was calculated as the ratio between leaf C content (to be accumulated to the leaf carbon pool, later on) and specific leaf density for the three pre-set vegetation groups – evergreens, tropical evergreens and summergreens. Thereafter, LAI values were derived using the equation accounting for GPP's dependency on leaf attributes. (Eq. 2).

3.4.3. Simulation protocol

The first simulation was initialized with a pre-set LAI value. Afterwards, at the end of each simulation, using the calculated NPP, the leaf area index was adjusted based on the function (Eq.2) adapted after the JULES model's approach (Joint UK Land Environment Simulator) (Clark et al. 2011). This leaf area index was then used as an input for the following iteration. The resulting GPP estimates were saved for further investigation.

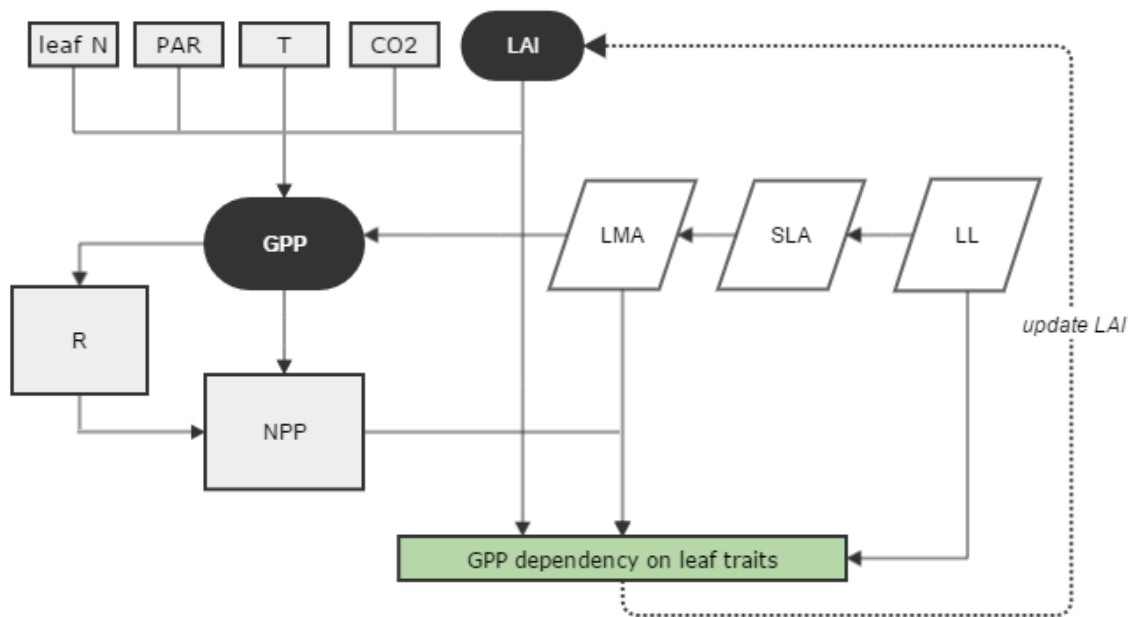


Figure 1. Conceptual representation of LEIA's structure. Trapezoids show leaf trait input parameters, key state variables are presented as black ovals, and grey rectangles show the LEIA's driving parameters.

3.5. Analysis of outputs

Having completed the sensitivity-like model simulations with the aim of determining the influence of varying leaf parameter, emergent GPP outputs were analysed using different statistical methods. LPJ-GUESS was ran with the pre-defined best guess parameter set to acquire the default output estimates that were used in the comparison.

The output data was found to be normally distributed (see Figure A5 in the Appendix). Upon confirming normal distribution in all cases, statistical tests were chosen accordingly. As a preliminary step, yearly mean values have been calculated by taking the mean of the output simulations to produce an average model simulation (one simulation spans 106 years). Afterwards, minimum, maximum, mean values as well as variance were computed. Once the output GPP estimates were sorted and pre-processed, the following descriptive statistical methods were applied.

The change in variance between the default and adjusted parameter set ups were studied using a two-sided Chi-squared variance test, applying a 5% significance level. To establish whether the means of different outputs are different from the initial mean, the two-sided Student's t-test was employed, applying a 5% significance level. For evaluating the change of mean values, using different parameter sets, an analysis of variance (ANOVA) test was used. To assess the spread of global GPP estimates, model outputs were plotted on a histogram. Additionally, since GPP output data followed a Gaussian distribution it was possible to plot a normal distribution with the specific group means to show how the distributions adjusting different parameters correspond to each other.

To evaluate the effect of parameter adjustment on different PFTs, the aforementioned statistical analyses were employed on summergreen and evergreen vegetation classes. BNE, BINE and TeBE PFTs were grouped representing evergreen vegetation, while the summergreen group consisted of BNS, IBS and TeBS PFT classes (for abbreviations see Table A1 in Appendix). The statistical evaluation process was repeated for all output groups, as well as Uncorrelated and Correlated cases.

4. Results

4.1. Frequency distribution

The first set of analyses determined the variance and mean of each group of GPP estimates, which is shown in Table 3. Thereafter, the frequency distribution was plotted for the Uncorrelated and Correlated cases, to be able to evaluate the change in the distribution of model estimates. Figure 2 presents, that varying leaf longevity for tropical evergreens resulted in a significantly wider spread of projections, than the other groups. It is apparent, that adjusting the leaf N parameter values gave the narrowest spread of estimates.

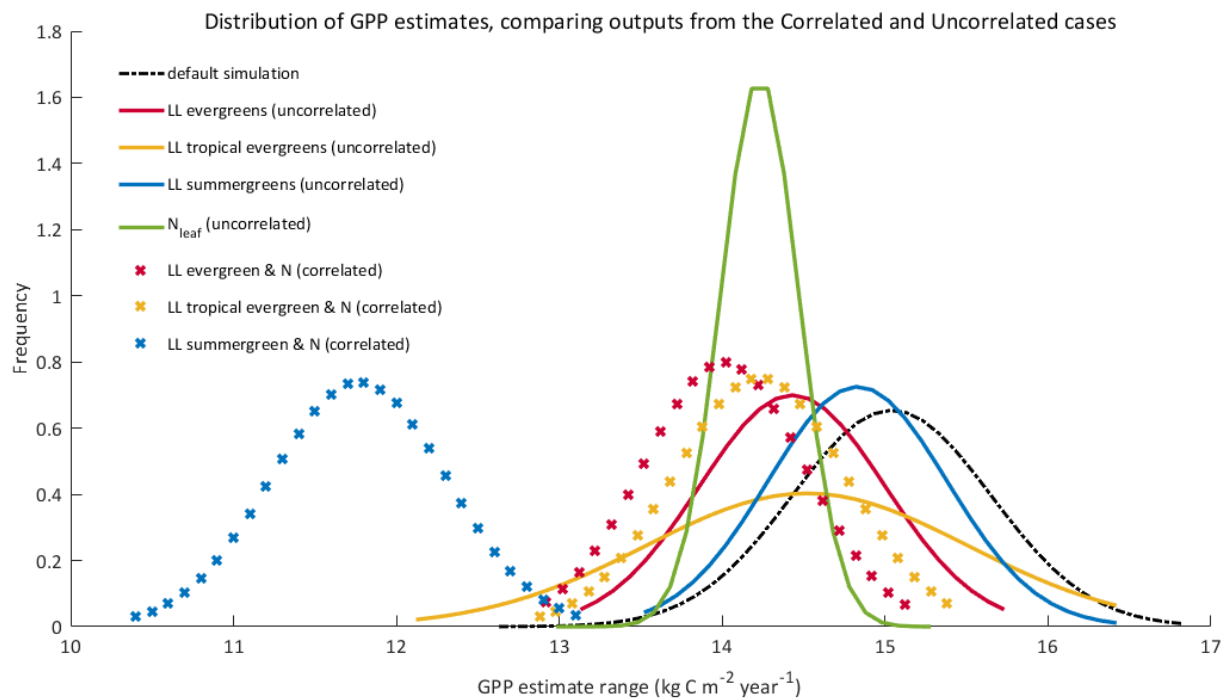


Figure 2. Frequency distribution of global annual GPP estimates, using the two defined methods. The default simulation is shown by the dashed black line.

4.2. Analysis of variances and means (Uncorrelated & Correlated cases)

Figure 3 compares the different group variances for the Correlated and Uncorrelated cases. From the chart, it is clear that varying leaf longevity for tropical evergreens resulted a significantly higher variance of outputs than the other three groups.

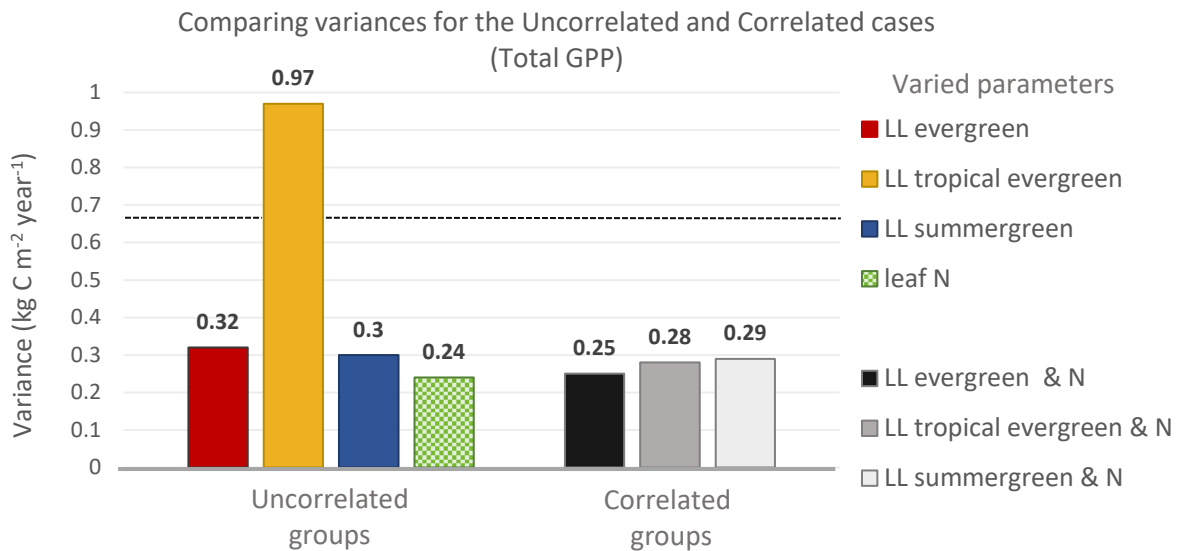


Figure 3. Comparing group variances between the Uncorrelated and Correlated cases. The dashed black line shows approximately the variance ($0.67 \text{ kg C m}^{-2} \text{ year}^{-1}$) of the default simulation.

Group-wise breakdown of the quantitative analysis is presented in Table 3. With the exception of varying LL for tropical evergreens, all group variances are in the range of $0.24\text{-}0.32 \text{ kg C m}^{-2} \text{ year}^{-1}$. This suggests that the variance in modelled estimates can be decreased using either the Uncorrelated or the Correlated methods. Looking at the group means, a two-sided Student's t-test revealed that the group means obtained by varying parameter values yielded a significantly different mean compared to the default simulation (see Table A11). Additionally, an ANOVA test showed that the Uncorrelated groups do not have a common mean (see Figure A7). An effective sample size test suggested that the applied sample numbers – 100 simulations per parameter for the Uncorrelated, and 50 pairs per group for the Correlated case – are suitable for further statistical analyses. Obtained variances from the GLOPNET Correlated case correspond well with the results of the Correlated case, using Reich et al. (1992) approach (see Table 3).

Table 3. Total global GPP estimates for the different groups.

Method	Adjusted parameters	Total GPP	
		mean ($\text{kg C m}^{-2} \text{ year}^{-1}$)	variance ($\text{kg C m}^{-2} \text{ year}^{-1}$)
Default simulation	-	15.04	0.67
Uncorrelated case	LL evergreens	14.43	0.32
	LL tropical evergreens	14.52	0.97
	LL summergreens	14.83	0.30
	Leaf N	14.23	0.24
Correlated case I. (covariance based on Reich et al. (1992))	LL evergreens & N	14.01	0.25
	LL tropical evergreens & N	14.23	0.28
	LL summergreens & N	11.77	0.29
Correlated case II. (covariance based on GLOPNET database)	LL evergreens & N	15.06	0.32
	LL tropical evergreens & N	14.73	0.27
	LL summergreens & N	14.35	0.27

4.3. PFT-specific analysis

Figure 4 shows the results attained from the PFT wise analysis of GPP outputs. The overall trend is a decrease in variance compared to the *default* variance of 0.81 and 0.45 kg C m⁻² year⁻¹ for the Evergreen and Summergreen groups respectively. Adjusting LL for summergreens causes a decrease in Evergreen GPP (3rd bar from left). The variation in evergreen leaf lifespan affects the summergreen GPP's behaviour. This finding may be explained by the fact that LPJ-GUESS includes an explicit representation of population dynamics, and thus changes in a vegetation type affect the behaviour of other PFTs in the same habitat, which may give a possible explanation for the patterns observed on Figure 4 and Figure 5. Varying LL for tropical evergreens shows a much different result than the other groups.

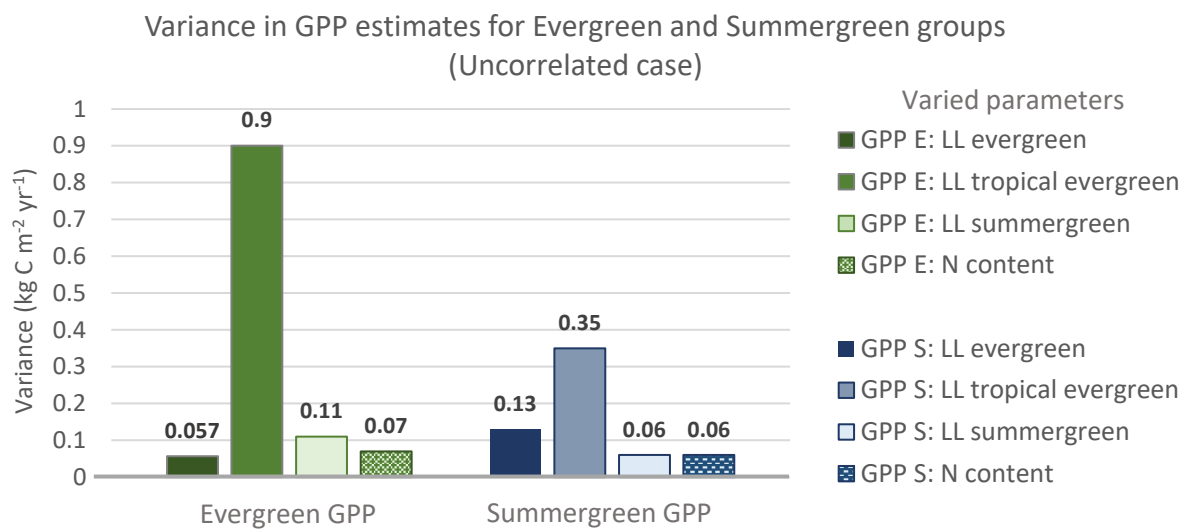


Figure 4. Analysis of evergreen and summergreen PFTs' GPP, as response of parameter adjustment. Bars show model simulations adjusting one trait's value at a time. - Uncorrelated case. (Default variance is 0.81 and 0.45 kg C m⁻² year⁻¹ for the Evergreen and Summergreen groups respectively.)

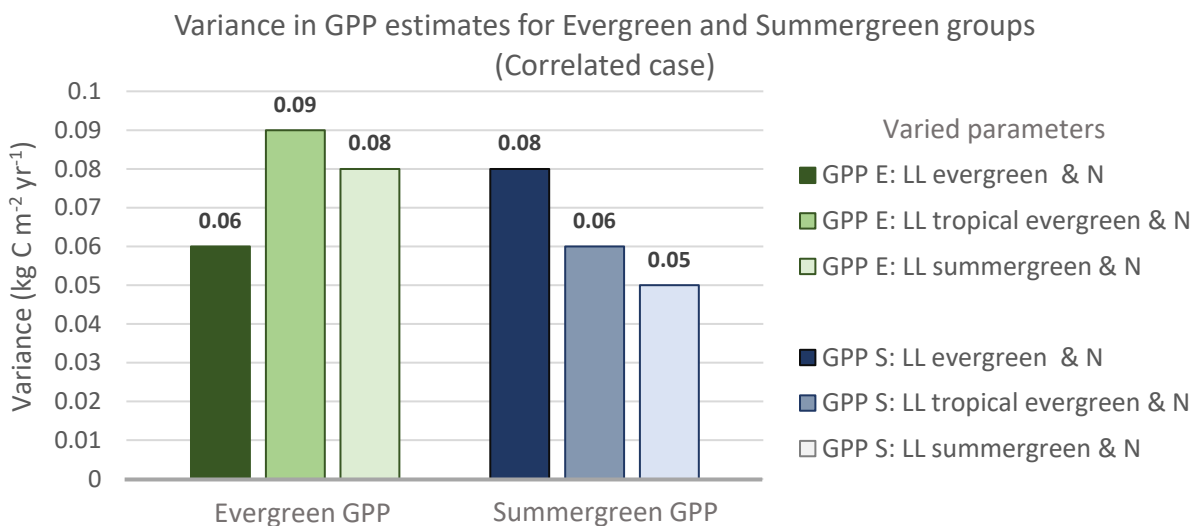


Figure 5. Analysis of evergreen and summergreen PFTs' GPP, as response of parameter adjustment. Bars showing different groups, where trait values were varied pairwise. - Correlated case. (Default variance is 0.81 and 0.45 kg C m⁻² year⁻¹ for the Evergreen and Summergreen groups respectively.)

As opposed to the Uncorrelated case, varying leaf longevity and N content did not yield a significant difference between the respective groups. Figures 4 and 5 indicate, that the magnitude of GPP variance is in the same range for Correlated and Uncorrelated cases, approximately between 0.05 and 0.09 kg C m⁻² year⁻¹, with the exception of varying LL for tropical evergreens individually.

The analysis of group variances regarding Tropical evergreen GPP (specified as the sum of GPP for TrBE and TriBE PFTs) showed that the initial variation of 0.07 decreased significantly when varying LL for tropical evergreens and leaf N parameters. Adjusting evergreen and summergreen LL did not yield significant changes. All derived groups had significantly different mean values than the default simulation. Since tropical GPP only accounts for a smaller fraction of the total GPP, this group is not further discussed in this study.

4.4. LEIA outputs: theoretical GPP range

The default simulation of the model – setting all analysed trait values as the best guess estimates – resulted in a global GPP estimate range between approximately 121 and 130 Pg C year⁻¹, that is comparable to global estimates presented in Table 1. Visual analysis of the results suggested that varying leaf trait values caused only a minor deviation in output estimates (for details see Table A10). A Chi-squared variance test confirmed that the group variances - varying leaf longevity for evergreens, tropical evergreens and summergreens as well as leaf N content - are not significantly different from the default variance. A t-test showed that the means are not significantly different from the default mean value. Analysing the Uncorrelated and Correlated outputs showed similar results. These findings made ground for further investigation of the model's behaviour, to be able to determine which elements are the most influencing on the global GPP estimates.

4.4.1. Adjusting LMA

Both in LPJ-GUESS and LEIA leaf mass per area is calculated as a function of leaf longevity (using Eq. 5 and Eq. 6 from Table A4), thus SLA was not varied initially. Seeing that the adjustment of leaf longevity did not yield considerable differences in LEIA outputs, Eq. 5 was taken out and LMA was varied across the potential range based on the GLOPNET database (see Table A3).

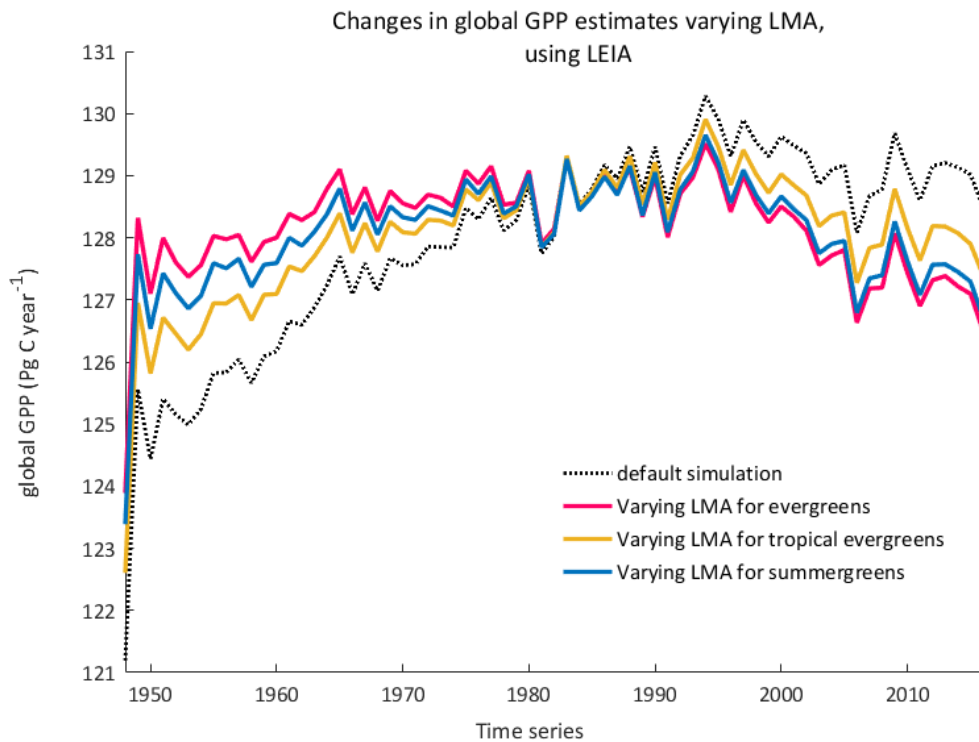


Figure 6. Changes in modelled global annual GPP, using varying LMA parameter in LEIA for different functional groups. Default simulation is shown by the dashed black line.

Figure 6 presents the GPP time series plotted with varying LMA parameter for different functional groups. Chi-squared variance test showed that adjusting LMA for evergreens tropical evergreens and summergreens significantly decreased the variance (p-values $5.63e-10$, $2.49e-05$ and $5.23e-09$, respectively). In case of changing evergreen LMA, the derived group mean was found statistically higher than the default simulation's mean, although the p-value of 0.0488 is just below the threshold significance level. The other two groups did not have differing means from the initial simulation.

4.5. Comparison of LPJ-GUESS and LEIA outputs

Although leaf attribute adjustments did not prove to yield significant differences in the derived outputs for LEIA, the two models' results were compared, as one of the objectives of the study was to examine how models with different structural set up respond to the changes of leaf trait parameter values. To achieve this, firstly relative group differences were computed, between each group's and the default simulation's variance. Afterwards, the calculated relative differences were averaged, and the initial group variances were compared to this average relative change. In this way, the direction of change in variances could be kept, and it is possible to compare the two models.

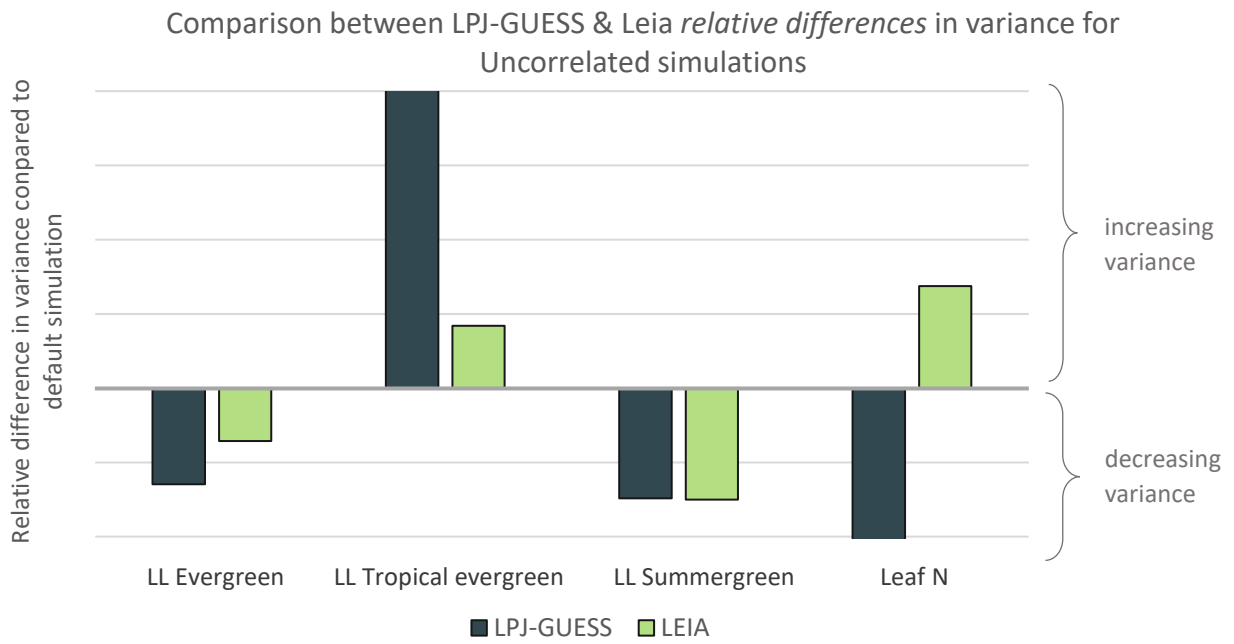


Figure 7. Comparison between relative variances for the analysed groups for models LPJ-GUESS and LEIA.

Figure 7 shows reduced variance in GPP estimates compared to the defaults simulation, when changing leaf longevity for evergreens and summergreens for both LPJ-GUESS and LEIA. The divergent behaviour of increased variance varying LL for tropical evergreens in LPJ-GUESS can also be seen in Figure 7, but interestingly, there is an increase in variance regarding this group in LEIA as well. Adjusting leaf N resulted the lowest variance for the DGVM, however variance increased in the idealised model.

5. Discussion

Affecting the net photosynthetic rate and the extent of modelled canopy area, each of the analysed leaf traits influence the simulated GPP estimates (Wang et al. 2012; Reich et al. 2007). Analyses on LPJ-GUESS outputs were conducted to determine the influence of leaf parameter adjustment on GPP estimates. Results show a general decrease in variances, when shifting parameter values, apart from adjusting leaf longevity for tropical evergreens, as seen in Figure 2. Data provided in Figure 3 shows that the magnitude of variances is similar varying values individually (Uncorrelated case) and simultaneously (Correlated case). This implies that a reduction of output variances can be achieved either by excluding as well as including covariance between the specified leaf traits. This can be attributed to the fact that LPJ-GUESS proved to be highly sensitive to the variation of leaf N content, thus shifting N along with a leaf longevity value also yield declining variance. Compared to other models, LPJ-GUESS's GPP predictions around 112-116 Pg C year⁻¹, are in the middle of the suggested range (Ahlström et al. 2012). In this case, opposed to the study of Wang et al. (2012), group means did change compared to the *default* simulation's mean, the group averages are lower than the initial mean. The lowest variation was found when varying leaf N values. These simulations resulted in a global GPP range of 165-174 Pg C year⁻¹, that is higher compared to other model estimates. Regarding the Correlated case, the general decrease in output variance of approximately 40% is higher than the 28% reduction observed for CABLE by Wang et al. (2012).

Comparing the frequency distributions based on Figure 2 for the Uncorrelated (continuous lines) and Correlated case (cross marked data series), it can be seen that varying leaf attributes resulted in GPP estimates with lower means than the default run in all cases. The spread of outputs is significantly different in the Uncorrelated case, meanwhile the association of leaf N content and leaf life span shows that the outcomes are similar between the three groups. An interesting feature to observe in Figure 2 is, that the simultaneous variation of leaf longevity for summergreens and N content resulted in a notably different distribution of output estimates, compared to the other groups. This may be explained by the fact that, when applying Eq.1 to assign leaf N values for the Correlated case, data points for the summergreen group are clustered at a narrow range of potential values. Figure A2 and Figure A3 present the LL and leaf N pairs created by using two different methods. Since summergreens shed their leaves at the end of the growing season, their group specific LL is close to the minimum of the potential LL range. Because of this feature, applying Eq.1 caused the derived leaf N values to be clustered, instead of showing an even distribution as evergreen and tropical evergreen data pairs do. Since low LL values does not follow a linear function, applying Eq.1 to create LL and leaf N could have led to a bias, with regard to the summergreen group.

5.1. Group specific patterns

Adjusting leaf longevity for evergreens and summergreens resulted in a similar group variance of GPP estimates. In contrast, varying leaf longevity for tropical evergreens shows a significantly different behaviour from the other groups, having a variance of $0.92 \text{ kg C m}^{-2} \text{ year}^{-1}$ (for p-values see Table A11). The underlying reason behind this can be the patch-based representation employed in LPJ-GUESS. Each of the 13 patches (sites) is characterised by a number of PFTs that could establish at that location. Out of the modelled patches only one includes tropical evergreen vegetation, which means that this vegetation group is under-represented in the model. This fact can explain the deviation of output variances compared to varying leaf lifespan for other vegetation groups.

This deviation regarding tropical evergreens is not observed evaluating LEIA simulations, since in this idealised model vegetation groups are treated uniformly, without differentiating their abundance or spatial extent. It is interesting though, that varying leaf longevity for tropical evergreens resulted in an increase of variance for both applied models. This behaviour varying LL for tropical evergreens might be explained by the fact that the potential LL range is the widest for tropical vegetation out of the three analysed groups. As reported by Ahlström et al. (2012) it is challenging to determine how tropical regions will respond to the changing climate. The applied models' results (see Figure 7) suggest that shifting parameter values for tropical evergreens may increase the uncertainty of model outputs.

Besides using Eq.1 (Correlated case I.) to create leaf longevity and leaf N pairs, another technique was tested as a validation step. Complete leaf lifespan-N pairs from the GLOPNET database were used as parameter values for LPJ-GUESS simulations (Correlated case II.). Because of the unequal and small number of pairs in each group, this method may be biased, and may not cover the entire potential range of values. Nevertheless, the derived group variances are in agreement with the ones obtained using Correlated case I. (see Figure A4).

As pointed out in section 4.1 and 5., output series acquired varying summergreen leaf longevity and leaf N values at the same time resulted in a significantly different frequency distribution than the other groups. Considering the characteristics of the summergreen group, looking at Figure A6 and examining the relationship between summergreen leaf lifespan and leaf N (Eq.1), we can infer that the shift in distribution towards lower GPP is linked to the fact that summergreens tend to have low N as well as low leaf longevity values, as it can be observed in Figure A2.

5.2. Vegetation dynamics

LPJ-GUESS employs a detailed patch based representation of vegetation, which means that besides the different biological and chemical processes, the model also considers competition between species for light and resources (Hickler et al. 2004). Containing an explicit representation of population dynamics - simulating establishment, growth and mortality - it can capture short term changes in the composition and structure of vegetation. These features suggest that changes in certain properties of a vegetation group (for instance adjusting leaf longevity values), is expected to cause a change in other groups' behaviour in the same ecosystem. PFT specific GPP is analysed to see the effect of parameter adjustment on the respective groups. Focusing on woody species, we assumed group-wise comparison of results for evergreen and summergreen groups is of interest. With regards to the Uncorrelated simulations, varying leaf longevity for evergreens and summergreens caused a decrease of variance in their respective GPP estimates. Furthermore, analysis of the results presented in Figure 4 and Figure 5 show, that shifting leaf longevity values for one of the two latter named groups affect the GPP outputs of the other group. The deviation of results for the tropical evergreen group can be observed examining evergreen and summergreen GPP, as well as it was seen for total GPP. Adjusting leaf N resulted the lowest group variances, just as observed when interpreting the general patterns. In terms of the Correlated case, co-varying leaf lifespan and leaf N yielded small difference in variance for both evergreen and summergreen GPP groups.

Because terrestrial ecosystems take up a large fraction of the anthropogenic CO₂, it is essential to include vegetation dynamics to represent vegetation-atmosphere interactions in an adequate and realistic manner. In this experiment, parameter values were chosen to be varied for one vegetation type at a time, to be able to analyse direct effects of the adjustment. Previous studies established that a large fraction of variation in leaf attribute values occurs within PFTs and not across them, which may imply that a dynamic parametrisation scheme may be fitting to include in models' structure (Kattge et al. 2011). In the future, it could be interesting to investigate the effect of altering leaf longevity and leaf N values at PFT level, since the changes in these group based characteristics could lead to a change in the competitiveness of certain PFTs or species in the same ecosystem.

5.3. Carbon-nitrogen interactions

As reported by Wang et al. (2010) amongst others, ecosystem productivity can be largely limited by N deficiency. N limitation may also act as a constraint to the predicted CO₂ fertilisation effect, therefore including the N cycle and C-N interactions in ecosystem models is highly important (Smith et al. 2014). Smith et al. (2014) observed a decline of global gross primary productivity when representing C-N interactions, compared to C-only LPJ-GUESS simulations (from 116 to 112 Pg C year⁻¹), and this estimate is lower than most of the other model predictions (Smith et al. 2014). Results of this study when altering leaf N content on its own, as well as together with leaf longevity show, that group means are lower than for the default simulation. Data presented in Table A11 from the both the Uncorrelated and Correlated case suggest that every group mean is significantly different from the default simulation's mean. This may indicate that the using *default* parameter sets, the model overestimates the global GPP.

Generally, nitrogen demand in LPJ-GUESS is determined by setting an optimal leaf N content value. This value is calculated by a linear relationship, in a way to maximize the carboxylation rate and thus the rate of C uptake (Smith et al. 2014). The relationship between $V_{c,max}$ and leaf N is highly important, it is discussed more in detail in section 5.4.1. Besides affecting the maximum carboxylation rate, leaf N also influences other variables, such as leaf respiration (Wårlind 2013).

In brief, LPJ-GUESS is found to be sensitive to the variation of leaf N parameter, however examining the underlying processes and causes that lead to the observed findings is out of the scope of this thesis.

LEIA computes the maximum carboxylation rate in a simpler way, as a linear function of leaf N content. Therefore, it is possible to investigate the effect of varying leaf N content on GPP estimates. Results from the Uncorrelated case contradict the declining variance trend observed in LPJ-GUESS. This deviation can be explained by the simplistic representation of N dependency in LEIA. The main reason for building LEIA was to be assign a theoretical GPP range, considering GPP's dependency on key leaf traits. LEIA was structured to be a simple idealised model to investigate causality and parameter adjustment's consequences, thus it cannot be used to examine what underlying factors lead to the change in the output estimates.

5.4. Maximum rate of carboxylation capacity

Several models – including LPJ-GUESS and LEIA - apply the Farquhar, von Caemmerer and Berry (FvCB) representation of photosynthesis, where the rate of C uptake is strongly dependent on the maximum carboxylation rate ($V_{c,max}$) (Rogers 2014). Since this variable can only be measured at small scale, it is a highly sensitive component of models, and contributes to the overall model uncertainty (Rogers 2014). There are various empirical, mechanistic or user-defined methods to compute maximum carboxylation rate. In LPJ-GUESS, $V_{c,max}$ is modelled in a mechanistic way to maximize the photosynthetic capacity and at the same time minimize the maintenance costs (Wårlind 2013). The idealized model applies a linear function, where the carboxylation is dependent on leaf N, as defined by the slope and intercept parameters (a, b) see Eq. 7 below.

$$V_{c,max} = a + b \times N_{leaf} \times LMA \quad (7)$$

Because of this straightforward representation, there is a possibility to directly analyse how the variation in trait values affect $V_{c,max}$, and thus the photosynthetic rate. The linear relationship applied in the LEIA (Eq. 7) is commonly incorporated in other models, like BETHY (Biosphere Energy Transfer Hydrology Scheme) (Kattge et al. 2009; Rogers 2014). Initially, literature based coefficient values were defined for the function, however model simulations showed a discrepancy between model outputs and literature observations. Hence, the intercept and slope parameters in the linear function needed to be tuned, to acquire representative $V_{c,max}$ estimates for the respective groups. Table 4 shows LEIA's behaviour using the literature based and adjusted parameter values, along with the derived variables. Looking at the modelled GPP range in Table 4, the difference between these two scenarios is considerable, since the literature based values provided much lower GPP estimates. Examining the consequence of varying leaf N and LMA components we concluded that, they only influence the emerging $V_{c,max}$ estimate in a small degree. For this reason, parameter a was calibrated, taking into consideration photosynthetic capacity estimates from a number of sources (see Table 4 and Table A7) (Monson and Baldocchi 2014; Rogers 2014).

Table 4. Slope and intercept parameter values, their influence on the predicted $V_{c,max}$ range and GPP range, for the evergreen vegetation group (Kattge et al. 2009).

Parameter setting (evergreens)	a ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	b ($\mu\text{mol CO}_2 \text{ g N}^{-1}\text{s}^{-1}$)	$V_{c,max}$ range ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	GPP range (Pg C year ⁻¹)
Kattge et al. (2009)	34	9.7	34.0023 -34.0258	69.33 - 75.60
adjusted in LEIA	38	20	38.0044 -38.0097	121.20 - 130.28

Adjusted parameter values are presented in Table A7. Modelled GPP range for LEIA is between 120 and 130 Pg C year⁻¹. Rogers (2014) reports that adjustments of parameters using an approach that

accounts for leaf N content when computing the carboxylation capacity rate may decrease $V_{c,max}$ estimates by approximately 30% for species with C3 photosynthetic pathway.

5.5. Leaf properties

In LEIA, the link between leaf properties and photosynthetic capacity is leaf area index (Eq.2). In this way, LAI acts as a measure of the total canopy area, whose changes influence the rate of carbon uptake. A comprehensive analysis of LAI measurements conducted by Asner et al. (2003) suggest, that LAI values predicted and used by LEIA are underestimated for each of the three vegetation groups, though the proportionality and difference between the groups is kept (LEIA estimate ranges 1.8-2.8, 1.4-1.8 and 1.2-1.4 for evergreen, tropical evergreen and summergreen groups respectively; whereas group-wise averaged LAI suggested by Asner et al. (2003) are as follows: 4.6, 4.8 and 3.25 for the respective groups) . A likely explanation for this may be that the leaf carbon content, that is the base of LAI calculation is underestimated. This feature could be further examined in the future.

LMA varies nearly 100-fold across species (Reich et al. 2007; Lusk et al. 2008) and since it is easy to measure and shows correlation to other key traits, LMA is studied extensively (Lusk et al. 2008). This index is of high importance from an ecological point of view, because it is sensitive to the changes in environmental conditions, such as light and water availability (Lusk et al. 2008; Reich et al. 2003). LMA is not adjusted directly in this LPJ-GUESS experiment, because SLA - the inverse of LMA - is calculated as a function of leaf longevity (see Eq. 6). To vary LMA directly would thus lead to a bias in regard of the outputs, and interpretation of their response to changing forcing values. The same equation (Eq.5) was used in LEIA, and to assess the influence of varying LMA, Eq. 5 was taken out, and LMA values were selected randomly from the known potential range, just as the other investigated traits were treated. Interestingly, LEIA shows higher sensitivity to the variation of LMA than either leaf longevity or leaf N content. This can be observed in Figure 6. Statistical analyses showed, that adjusting LMA for evergreens, tropical evergreens and summergreens induced a decrease in variance in LEIA. Additionally, altering LMA for the evergreen group influenced the group mean significantly. These findings indicate that accounting for leaf traits, specifically leaf lifespan in a more straightforward way, rather than including traits within complex functions would yield a larger degree change in LEIA outputs. Another possible way of approximating LMA was suggested by Poorter et al. (2009), which could be considered in case LEIA is further developed. LMA can be computed as a function of leaf density (LD) and leaf volume to area ratio (LVA). Of course, these indices would also be approximated, that introduces another source of uncertainty in model parametrisation. Poorter et al. (2009) claims that LD and LVA values can be set based on available observational data. In case, the calculation of LMA would be changed and Eq.5 excluded, we should investigate alternative methods to account for

leaf longevity to ensure that varying multiple parameters at a time would be possible. For the purpose of this project, Eq. 5 was found suitable and therefore applied as part of the analysis.

5.6. Comparison of models

Having a straightforward and simplified representation of processes makes it possible to analyse cause and effect relationships using LEIA. Moreover, it is also possible to determine which factors have the greatest influence on GPP estimates. However, the applied empirical and mechanical relationships require parametrisation of driving variables and parameters, which introduces sources of errors. Therefore, the output estimates of LEIA have a very high uncertainty.

Comparing LEIA and LPJ-GUESS performance qualitatively shows the same trends in changes, in case varying leaf longevity parameter values. Although the degree of variance decline is significant for LPJ-GUESS in this study (see Table A11), further investigation is needed to determine if the suggested approach is reasonable and yield the desired effects, as to avoid adding unnecessary complexity to models.

Evaluating the model's performance highlighted that LEIA is more sensitive to the change in driving values - specifically for daylength and parametrisation of carboxylation capacity - than the adjustment in leaf trait values. Because of this reason the deviation in the output estimates for changes in leaf parameter values is significantly lower (Table A10), than the ones observed for LPJ-GUESS (Table 3).

Differences in absolute changes in LPJ-GUESS and LEIA should be compared to each other with consideration, since the degree of change regarding GPP estimate ranges was considerably higher for LPJ-GUESS (comparing Table 3 and Table A10). A possible explanation for this can be found looking at the models' structure and included processes. As mentioned earlier, the DGVM applies a complex representation of the C-cycle, including atmospheric-plant interactions. The mechanistic approaches enable LPJ-GUESS to simulate natural conditions more accurately, but at the same time make the model highly nonlinear. Consequently, it is extremely hard to track the effect and feedbacks related to the adjustment made for instance for a driving variable. The smaller scale changes observed using LEIA suggest, that the alteration of leaf traits induces a negative feedback loop, and thus the changes in the derived variables are minor. Aside from this, statistical tests confirmed that the adjustments did not result in significant changes in GPP estimates variance and mean in LEIA. On the other hand, analysing relative changes compared to default simulations for each model provides a way to examine the models' behaviour. Figure 7 implies that the two models have similar responses to the variation of leaf longevity input parameter values. These findings indicate the presented models with different structure show similar responses to the variation of leaf lifespan parameter values.

The theoretical predicted GPP range of LEIA between 120 and 130 Pg C year⁻¹ is lower than the mean GPP estimates of 174 Pg C year⁻¹ for the default simulation, using LPJ-GUESS. This indicates, that LEIA underestimates annual GPP, compared to the DGVM. Predictions of LPJ-GUESS with the applied set-up and driving parameters are at the higher end of the suggested GPP range, presented in Table 1. Mean GPP estimates for evergreen and tropical evergreen groups are lower than the default simulation. The most significant change in global GPP was observed varying leaf N, resulting in a mean GPP estimate of 165 Pg C year⁻¹.

5.7. Future work

At present, bearing in mind the specific assumptions and limitations, LEIA can be used for diagnostic purposes. In the future, LEIA can be further developed and even adapted for site-specific use. This would make it possible to compare model outputs to measurement data, and calibrate the model for more robust results. LEIA's insensitivity to leaf parameters has already been mentioned previously, but aside some drawbacks derived from the simplistic and idealistic structure, LEIA provided an opportunity to examine what are the important factors influencing GPP estimates. Temporal scale of the simulation could be defined as monthly and the length of the analysis could be if extended, given longer climatic input datasets. In this study, spatial variation in GPP variance is not accounted for, instead a generalized global view is applied. Focusing on woody PFTs, the influence of parameter adjustment on C3 and C4 grasses was not analysed, this may be of interest to look at in the future. The selection of parameters from the pre-set range can be further refined by for instance defining values that are commonly occurring to have a higher change of being selected. Even though an effective sample size test suggested that the used sample sizes are adequate for statistical testing, more model simulations would ensure the realistic interpretation of results.

Knowledge of the variation and relationship between key leaf traits may be used to adapt the strict PFT wise vegetation classification scheme into one that uses a continuous scale regarding for instance trait properties (Reich et al. 2007). As Rogers (2014) states having extensive and continuously expanding leaf trait databases available - such as GLOPNET and TRY (Kattge et al. 2011; Wright and Reich 2011) - can help to make a more uniform parametrization approach amongst different models, and lead to better constrained model outputs. This could include, that some of the currently constant PFT parameters, such as leaf longevity can be represented as state variable, instead of having constant pre-set values. Prentice et al. (2015) proposes that advances should be made to develop a stochastic parametrization scheme, as setting constant attributes may lead to a misfit between simulation output and observational data. Fitting a probability density function based on measurements for instance of different leaf traits, and then select parameter values within the PDF for each model run poses a potential realization of this approach that could be tested in the future (Prentice et al. 2015).

6. Conclusion

Main findings of this study can be summarized as follows:

- › Correlated and Uncorrelated LPJ-GUESS simulations indicate the same magnitude decrease in GPP estimates' variance.
- › Varying leaf N resulted in the most significance decrease in GPP variance.
- › LEIA shows low sensitivity to the variation of leaf traits parameter values, however is able to capture the direction of changes observed using LPJ-GUESS reasonably well.

State-of-the-art ecosystem models - such as LPJ-GUESS - include a complex representation of the most important ecosystem processes. Recent research is directed at providing more robust outputs, and at the same time developing the models' ability to resemble natural processes as closely as possible. Despite this, modelled entities can never be perfect, because models by nature are simplification of reality. Using the knowledge of the relationship between key leaf traits offers a more mechanistic, rather than empirical approach when assigning values for driving parameter values. Besides the qualitative factors, these adjustments may help ecosystem models to better capture the complexity of natural systems and improve the 'quality' of predictions.

Prentice et al. (2015) suggests, that besides developing more sophisticated benchmarking and data-assimilation techniques as to improve models' performance, more attention should be directed at reviewing the models' structure itself. They highlight the idea of analysing the implementation of a 'stochastic parametrisation' approach. Having extensive plant trait datasets and sufficient data on global GPP available, examining stochastic parametrisation of PFTs' leaf attributes and its effect on GPP estimates is a straightforward opportunity to improve models along with other methods like calibration techniques or data-assimilation (Prentice et al. 2015).

Based on the results of this study, varying key leaf trait values can lead to a decrease of variance in model outputs, consequently increased robustness of model predictions and less uncertainty derived from imperfect parametrization process.

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8. Appendix

8.1. Abbreviations

CABLE: Australian Community Atmosphere Biosphere Land Exchange model

DGVM: dynamic global vegetation model

GHG: greenhouse gases

GPP: gross primary production, C assimilated during photosynthesis

IPCC: Intergovernmental Panel on Climate Change

JULES: Joint UK Land Environment Simulator

LAI: leaf area index

LEIA: LEaf Index Analysis model, accounting for GPP's dependency on leaf traits

LL: leaf longevity or leaf lifespan in years

LMA: leaf mass per area (kg m^{-2})

LPJ-GUESS: Lund-Potsdam-Jena General Ecosystem Simulator, dynamic global vegetation model

N_{leaf} : leaf nitrogen content

NPP: net primary production

PFT: plant functional types

SLA: specific leaf area, ratio of the one-sided surface area to leaf carbon mass, $\text{m}^2 \text{kg C}^{-1}$

SLD: specific leaf density, $\text{kg C} / \text{m}^2 \text{m}^{-2} \text{LAI}$

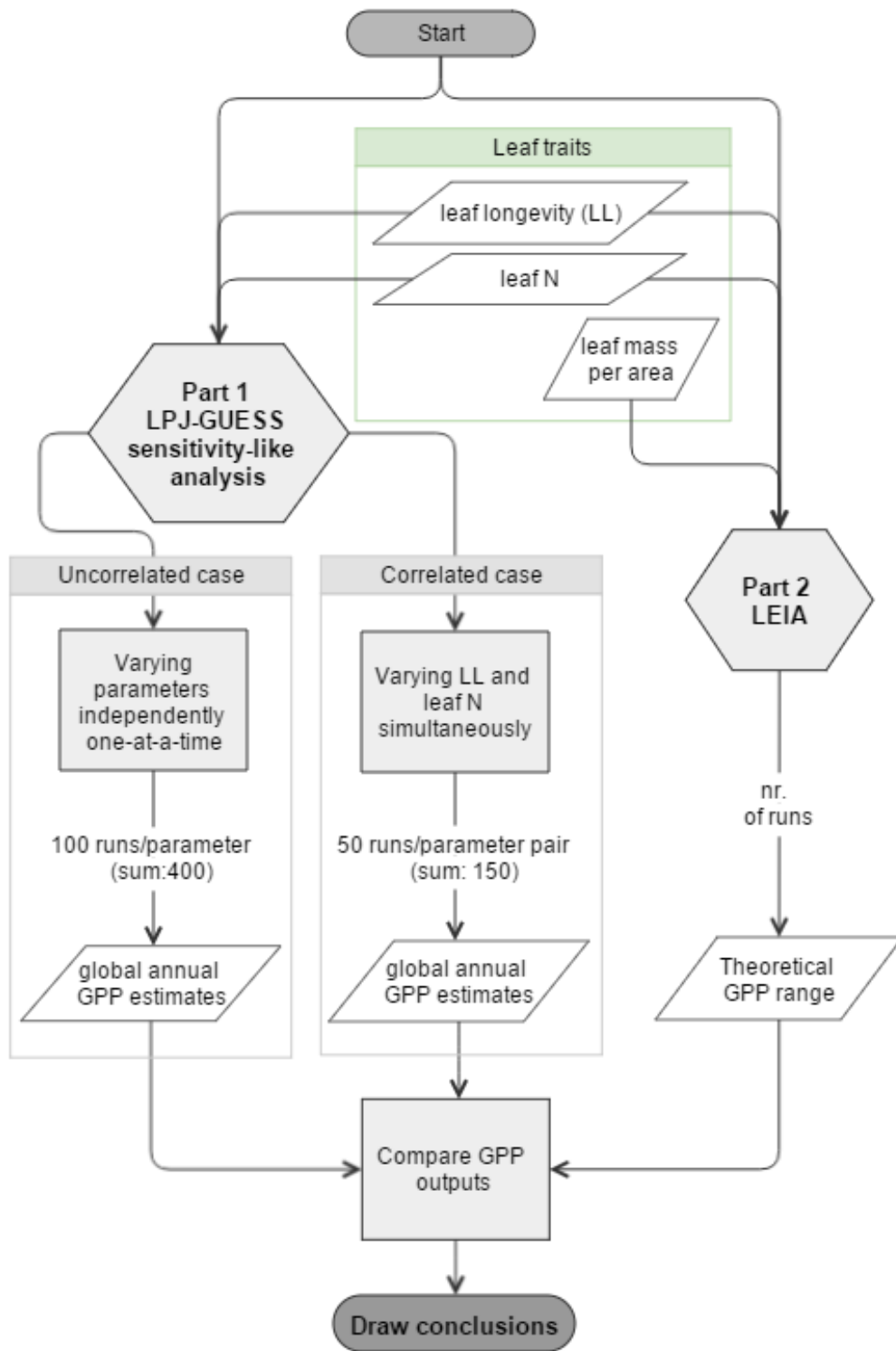


Figure A1: Flowchart of project workflow and expected outcomes.

8.2. Vegetation classification used in Part 1

Table A1. PFT specific information, and classification of PFTs based on phenological attributes.

PFT	Main vegetation group (<i>LL</i> adjustment)	Distribution	Growth form	Leaf phenology	Shade-tolerance	Photo-synthetic pathway
BNE	evergreen	boreal	needle-leaved tree	evergreen	tolerant	C3
BINE		boreal	needle-leaved tree		intolerant	
TeBE		temperate	broadleaved tree		tolerant	
BNS	summergreen	boreal	needle-leaved tree	summer-green	intolerant	
TeBS		temperate	broadleaved tree		tolerant	
IBS		boreal/temperate	broadleaved tree		intolerant	
TrBE	tropical evergreen	tropical	broadleaved tree	evergreen	tolerant	
TrIBE		tropical	broadleaved tree		intolerant	
TrBR	tropical raingreen	tropical	broadleaved tree	raingreen	intolerant	
C3G	parameters not varied (set as default)	boreal/temperate	grass	summer-green/ raingreen	intolerant	
C4G		tropical	grass		intolerant	C4

Table A2. Vegetation classification based on leaf phenology, used to set ranges based on GLOPNET dataset (Wright et al. 2004).

Original grouping	Adjusted grouping
evergreen/needleleaf	evergreen
evergreen/broadleaf	tropical evergreen
deciduous/broadleaf deciduous/needleleaf	summergreen

8.3. Relationship between leaf traits and leaf longevity

The following linear equation was used to calculate leaf N parameter values, as a function of leaf lifespan. Leaf longevity was used as an independent variable (x) and leaf N content as a dependent variable (y).

$$\log(N_{leaf}) = 1.61 - 0.31 \times \log(LL) \quad (1)$$

where N_{leaf} is in mg g^{-1} and LL is in months. Units were aligned to common units. It can be seen in Figure A2, that using the linear function the calculated leaf longevity and leaf N pairs are spread along the potential range for the respective groups. Looking at Figure A3, it seems that using the complete pairs from GLOPNET database group lifespan values, especially for summergreens are clustered close to the lower end of the possible range. These findings can explain the divergent trend observed when varying leaf longevity for summergreens and leaf N content at the same time.

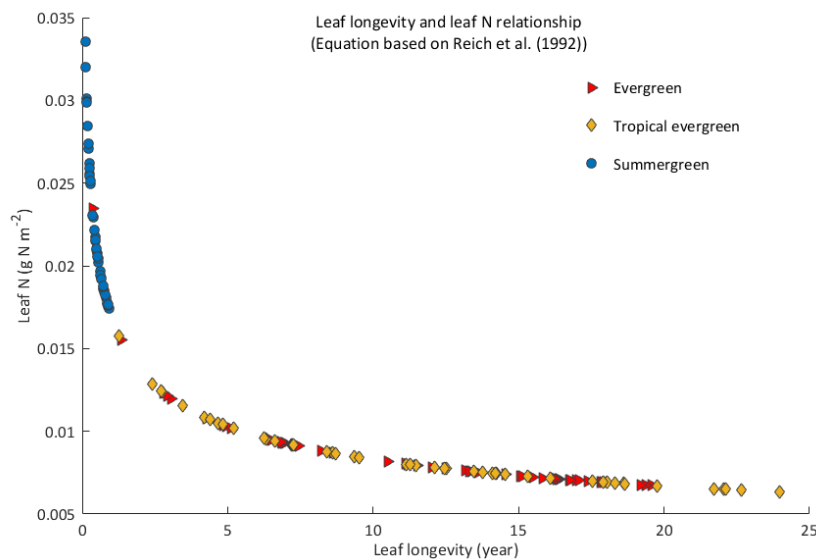


Figure A2: Relationship between leaf lifespan and leaf N content, based on Reich et al. (1992).

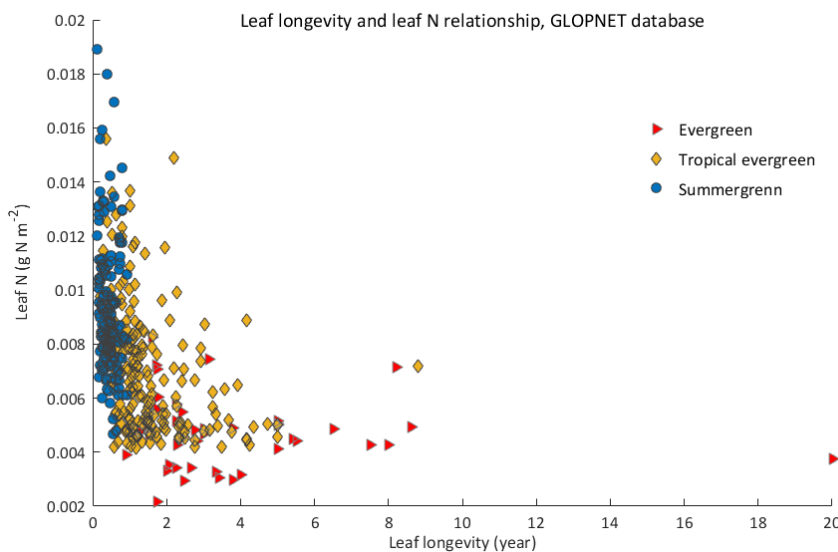


Figure A3: Relationship between leaf lifespan and leaf N content, based on the GLOPNET database (Wright and Reich 2011).

8.4. Comparison of parameter values selecting methods for the Correlated case

The left side of Figure A4. presents the variance of outputs obtained by selecting pairs from the GLOPNET trait database. To the right, bars show output variances calculated considering the covariance between LL and leaf N (using Eq.1). The two techniques yield nearly identical group variances.

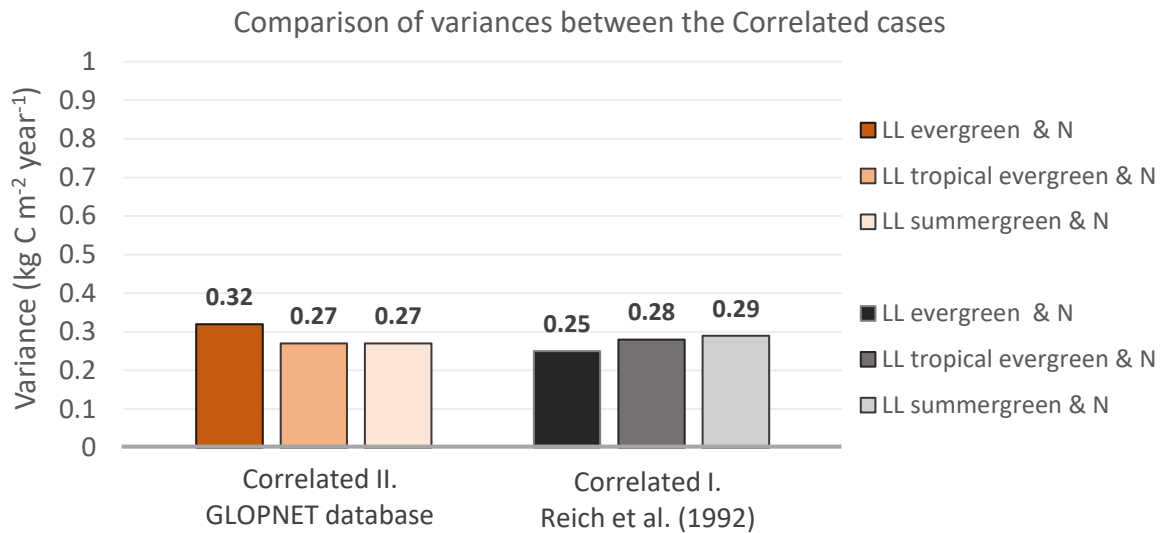


Figure A4: Comparison of variances between the Correlated cases.

8.5. Testing normality of model outputs

Normal distribution was confirmed by the normal probability plot, since the model outputs follow a linear trend, with GPP estimates aligned in agreement with the reference line (see Figure A5).

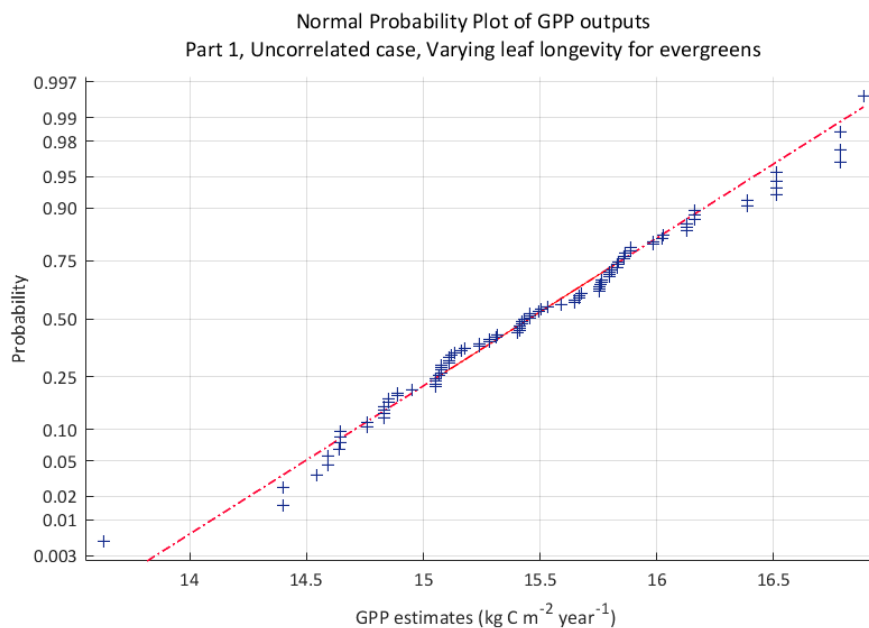


Figure A5. Normal probability plot, showing the distribution of GPP outputs from LPJ-GUESS for a simulation group using the Uncorrelated case. Normal distribution was confirmed for all the analysed groups for Uncorrelated, as well as Correlated cases, and statistical tests were chosen accordingly.

8.6. Relationship between leaf longevity and leaf mass per area

Leaf mass per area was taken as the inverse of SLA, computed with Eq. 5 as a function of leaf longevity. An interesting feature to note is that computed evergreen LMA values are in fact lower than the minimum values suggested by the literature.

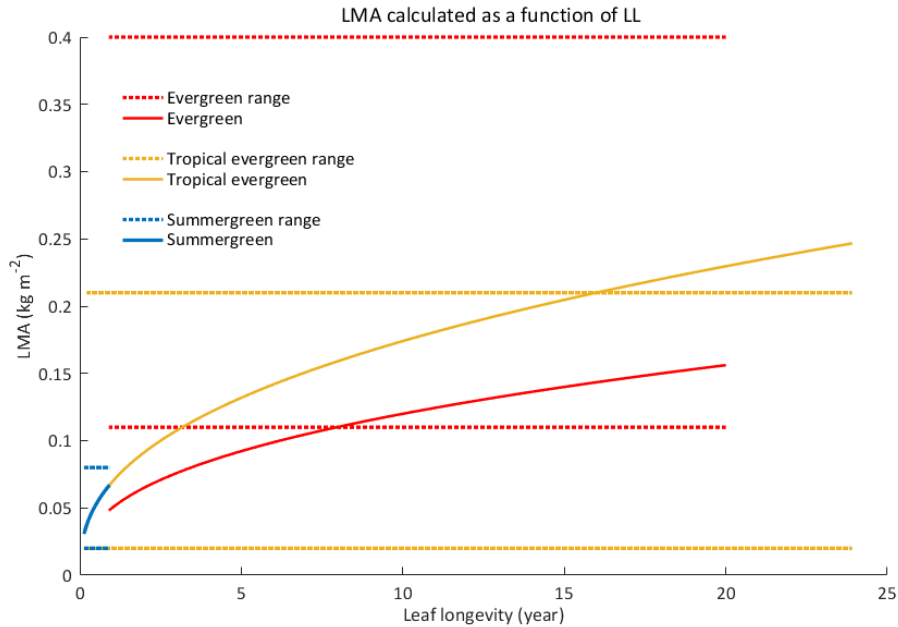


Figure A6. Visualizing the relationship between LMA and leaf longevity.

Table A3. LMA ranges based on the GLOPNET dataset Wright and Reich (2011) and Poorter et al. (2009).

<i>LMA</i> estimates (kg m^{-2})				
Vegetation group	GLOPNET (Wright et al. 2004)			Poorter et al. (2009)
	min.	max.	mean	range
evergreen	0.11	0.78	0.32	0.08 – 0.4
tropical evergreen	0.02	0.73	0.18	0.03 – 0.15
summergreen	0.02	0.21	0.08	0.05 – 0.11

8.7. LEIA structure & description

Since the main aim of the idealised model was to be able to track and analyse the result of adjusting certain leaf traits and evaluate the effect on GPP estimates, simplicity was the key factor when deciding which approach and functions to include in the model.

To estimate GPP, a set of parameters and constants values were used, whose values was set as *best guess estimates* based on literature and previous studies (see Table A5 – A8.). These parameters that did not directly affect the relationship between leaf traits and the rate of photosynthesis were set as constants not to add unnecessary complexity to the model. Incoming photosynthetically active

radiation at the top of the canopy was approximated as $700 \mu\text{mol m}^{-2} \text{s}^{-1}$. The absorbed radiation was then computed using Eq. 9, following Beer's law. Leaf longevity value is chosen the same way, as for Part 1. Thereafter, specific leaf area was computed using the relationship between leaf lifespan, N content and SLA (see Eq.5). Leaf mass per area was taken as the inverse of SLA, and along with leaf N content affects the maximum rate of Rubisco activity. LAI influences the fraction of photosynthetically active radiation, that is accounted for at the determination of the light limited photosynthetic rate. The maximum rate of potential electron transport is roughly the 1.67 times higher than the maximum rate of Rubisco activity (Monson and Baldocchi 2014), in this project is estimated as the double of $V_{c,max}$, following Wang et al. (2012) (see Eq. 8). For the sake of simplification, daylength, the number of hours with sunlight per day is set as a constant. Upon computing the GPP for the defined vegetation groups (evergreens, summergreens and tropical evergreens), the total global GPP was reckoned as the sum of the three GPP fractions. Respiration was stated as the half of the total GPP, as a rough estimation. Net primary production was determined by subtracting ecosystem respiration from the total GPP.

The link between carbon uptake capacity and leaf properties in LEIA is the leaf area index. Using Eq. 2 the primarily computed NPP is accounted for to determine how the leaf area index is affected at each model iteration. At the end of each simulation (year), one third of NPP is allocated to the existing leaf carbon pool, this fraction representing the biomass growth component. Biomass loss is computed by considering leaf mortality. Ambient temperature's effect on leaf loss rate was accounted for in the model by setting cold temperature limit of 5°C . Monthly temperatures were compared to this value and litterfall was adjusted accordingly. Applying Eq. 2 the acquired LAI is then used as an input parameter at the upcoming model simulation.

As of now the model is set for global scale, however by adjusting the driving parameters it can easily be converted for site-specific use. The advantage of this would be that outputs could be validated against observations, and if needed the model could be calibrated, in order to provide more robust estimates.

Table A4. Equations used in LEIA.

$$LAI = Leaf_C^{new} - \frac{(\gamma_{lm} \times LAI_{old} / 366)}{SLD} \quad (2)$$

$$\Gamma^* = \frac{O_2}{2\tau} \quad (3)$$

$$C_i = \lambda \times C_a \quad (4)$$

$$SLA = 0.2 \times g(\beta_0 + \beta_1 \log_{10} (12 \times LL)) \quad (5)$$

$$g(p) = 10^p$$

$$LMA = \frac{1}{SLA} \quad (6)$$

$$V_{c,max} = a + b \times N_{leaf} \times LMA \quad (7)$$

$$J_{max} = 2 \times V_{c,max} \quad (8)$$

$$I = I_0 \times e^{-k \times LAI} \quad (9)$$

$$J = \frac{I + J_{max} - \sqrt{(I + J_{max})^2 - 4 \times \theta \times I \times J_{max}}}{2\theta} \quad (10)$$

$$J_E = \alpha \times \frac{(C_i - \Gamma^*)}{4C_i + 8\Gamma^*} \times J \quad (11)$$

$$J_C = \frac{(C_i - \Gamma^*)}{C_i + K_c (1 + \frac{O_2}{K_o})} \times V_{c,max} \quad (12)$$

$$GPP = \frac{(J_E + J_C - \sqrt{(J_E + J_C) \times (J_E + J_C) - 4 \theta \times J_E \times J_C})}{2\theta} \times \text{daylength} \quad (13)$$

$$R = \frac{GPP}{2} \quad (14)$$

$$NPP = GPP - R \quad (15)$$

$$LAI_0 = \frac{Leaf_{C,0}}{SLD} \quad (16)$$

$$Leaf_C^{new} = \frac{NPP}{3} + Leaf_C^{old} \quad (17)$$

$$\gamma_{lm} = 0.25 \text{ or } \gamma_0 \times (1 + d_T(T_{cold} - T)) \text{ depending on air temperature} \quad (18)$$

Table A5. Parameters used in LEIA.

Parameter	Description	Value	Unit (source)	Unit (model)	source
Γ^*	compensation point	Eq. 3	-	-	1.
θ	empirical curvature factor	0.7	-	-	2.
K_o	Michaelis constant of CO ₂	30	kPa	kPa	
K_c	inhibition constant of CO ₂	0.030	Pa	kPa	
<i>daylength</i>	sunlit hours per day	12	-	h	
O_2	partial pressure of O ₂	21	kPa	kPa	
τ	CO ₂ /O ₂ specificity ratio	2600	-	-	
I_0	incoming solar radiation at the top of the canopy	700	$\mu\text{mol m}^{-2} \text{s}^{-1}$		-
C_a	ambient CO ₂ conc.	measured	$\mu\text{mol mol}^{-1}$	kPa	3.
λ	ci/ca ratio	0.7	-	-	2.
α	intrinsic quantum efficiency of CO ₂ uptake	0.08	-	-	1.
a	empirical coefficient, intercept	See Table A7. (used in Eq.7)			4.
b	empirical coefficient, slope				
k	extinction coefficient	0.5	-	-	1.
LL	leaf longevity	pre-defined	year		-
N_{leaf}	leaf nitrogen content	pre-defined	gN gC^{-1}		-
T_{cold}	temperature threshold for leaf loss because of cold stress	5	$^{\circ}\text{C}$		6.
β_0	regression coefficients	See Table A8.			5.
β_1					
$CMASS$	molar mass of carbon	12		-	1.
γ_0	minimum turnover rate	360 days ⁻¹		7.	
d_T	rate of change in turnover as a function of T	360 days K ⁻¹			
SLD	specific leaf density	See Table A6.			
$Leaf_{C,0}$	initial leaf C	kg C m^{-2}			

Sources: 1. Haxeltine and Prentice (1996); 2. Collatz et al. (1991); 3. NOAA, Mauna Loa Observatory (2007); 4. Kattge et al. (2009); 5. Smith et al. (2014); 6. Arora and Boer (2005); 7. Clark et al. (2011)

Table A6. Specific leaf density parameter values, based on vegetation groups, from Clark et al. (2011).

Vegetation group	SLD ($\text{kg C} / \text{m}^2 \text{m}^{-2} \text{LAI}$)
summergreen	0.0375
tropical evergreen	0.05
evergreen	0.025

Table A7. Intercept (a) and slope (b) coefficients for summergreen, evergreen and tropical evergreen vegetation types (grouped based on leaf phenology). Adapted after Kattge et al. (2009).

Vegetation group	a ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	b ($\mu\text{mol CO}_2 \text{ g N}^{-1}\text{s}^{-1}$)
summergreen	29	18
tropical evergreen	18	10
evergreen	38	20

Table A8. Regression coefficients β_0 and β_1 for summergreen, evergreen and tropical evergreen vegetation types Smith et al. (2014), used in Eq.4.

Vegetation group		β_0	β_1
this study	Smith et al. (2014)		
summergreen	broadleaved	2.29	-0.40
tropical evergreen			
evergreen	needleleaved	2.41	-0.38

Table A9: Derived variables in LEIA.

Variable	Description	Unit	Source
C_i	intercellular CO ₂ conc.	kPa	Eq.4
I	absorbed photosynthetically active radiation	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Eq.9
SLA	specific leaf area	$\text{m}^2 \text{ kg C}^{-1}$	Eq.5
LMA	leaf mass per area	kg m^{-2}	Eq.6
LAI_0	one-sided leaf area index, initial value	$\text{m}^2 \text{ m}^{-2}$	Eq.16
$V_{c,max}$	maximum rate of Rubisco activity at 25°C	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Eq.7
J_{max}	maximum rate of potential electron transport	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Eq.8
J	e ⁻ transport rate	$\text{mol electrons m}^{-2} \text{ s}^{-1}$	Eq.10
J_E	light-limited component	$\mu\text{mol m}^2 \text{ s}^{-1}$	Eq.11
J_C	Rubisco-limited component	$\mu\text{mol m}^2 \text{ s}^{-1}$	Eq.12
GPP	photosynthesis	$\mu\text{mol m}^2 \text{ s}^{-1}$	Eq.13
R	ecosystem respiration	$\mu\text{mol m}^2 \text{ s}^{-1}$	Eq.14
NPP	net primary productivity	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Eq.15
γ_{lm}	leaf turnover rate	360 year^{-1}	Eq.18

Table A10: Result of LEIA simulations (the presented values are not scaled up)

Statistical analyses of LEIA simulations				
Varied parameters	variance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	p-value	mean ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	p-value
Uncorrelated simulations				
default simulation	0.085295096	-	22.63980525	-
LL Evergreens	0.085345494	0.9582	22.64111317	0.9704
LL Tropical evergreens	0.085406446	0.9534	22.64139614	0.9640
LL Summergreens	0.085314554	0.9536	22.63977838	0.9994
N	0.085427348	0.9796	22.64286136	0.9308
Correlated simulations				
LL Evergreens & N	0.085289921	0.9606	22.6429251	0.9295
LL Tropical evergreens & N	0.085209538	0.9538	22.64240192	0.9413
LL Summergreens & N	0.085314554	0.9475	22.65133662	0.7441

Table A11: Significance of changes in variance and mean observed for LPJ-GUESS simulations (Group variances and means are presented in Table 3).

Statistical analyses of LPJ-GUESS simulations			
Method	Varied parameters	p-value	
		Variance (Chi-squared variance test)	Mean (Two-sided t-test)
Uncorrelated case	LL Evergreens	3.1489e-06	2.8075e-19
	LL Tropical evergreens	0.0037	5.4135e-07
	LL Summergreens	4.8718e-07	1.7038e-04
	N	1.5387e-10	1.8987e-32
Correlated case	LL Evergreens & N	1.2050e-09	1.2076e-39
	LL Tropical evergreens & N	3.0414e-08	1.0130e-29
	LL Summergreens & N	9.0827e-08	3.4507e-85

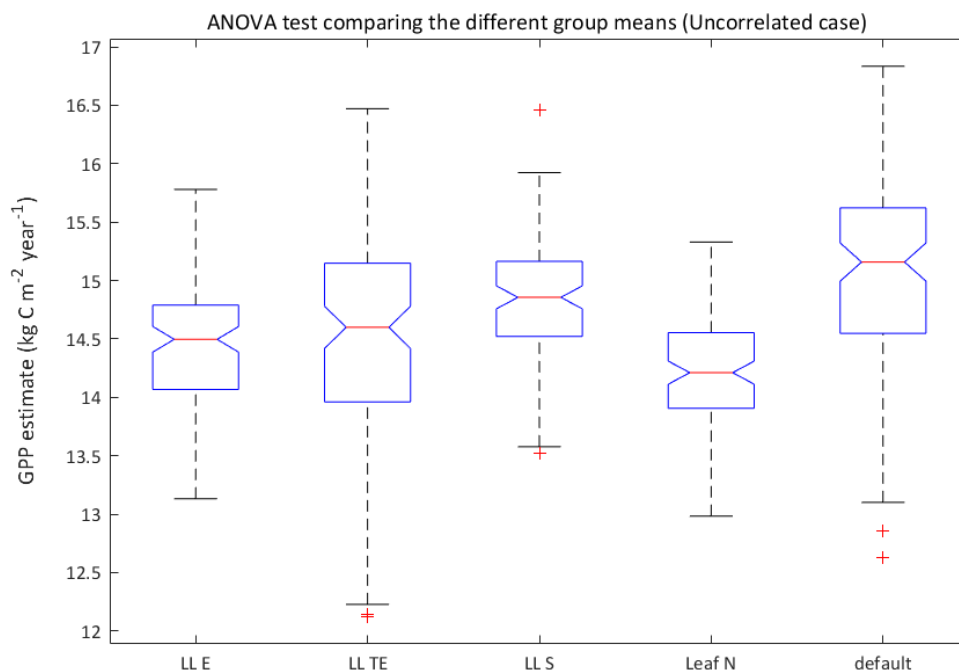


Figure A7. ANOVA analysis of the relationship between the default and Uncorrelated case group mean values. Group divisions (varied parameters) are shown on the x axis. Based on the statistical test, the groups do not have a common mean.

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