

Accurate representation of leaf longevity is important for simulating ecosystem carbon cycle



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Abstract

Leaf longevity and leaf turnover rate are important plant traits relating to plant growth, leaf photosynthesis and respiration, plant canopy dynamic and many other factors, but dynamic global vegetation models only set inaccurate values for these factors. In this study, we firstly investigated the leaf longevity at major vegetation types based on 418 field measurements from around the world. By replacing the default leaf longevity in the Lund-Potsdam-Jena model (LPJ) with the revised values, we examined the changes in simulated carbon cycle caused by the revised parameters. The results suggested that the compiled observations of leaf longevity were significantly different from the default values in LPJ. Both the vegetation production and respiration of the simulated natural ecosystems showed significant changes based on the revised leaf longevity compared with the predictions developed using default model parameters. Of all of the variables, the aboveground and belowground litter pools showed the largest changes (about 10% globally). Globally, the default parameters induced a significant overestimation of terrestrial carbon sink by 3%, compared with a simulation using the revised parameters. Furthermore, the uncertainties in leaf longevity caused various uncertainties (5–30%) in the simulated carbon fluxes and carbon pools. The offset of biases in intermediate variables might result in rational final model outputs. Overall, more accurate leaf longevity are critical for simulating the vegetation distribution and ecosystem carbon cycle.

Zusammenfassung

Die Lebensdauer der Blätter und ihre Turnover-Rate sind wichtige Merkmale von Pflanzen. Sie stehen in Beziehung zum Pflanzenwachstum, zu Photosynthese und Respiration der Blätter, zur Kronendynamik und vielen anderen Faktoren, aber dynamische, globale Vegetationsmodelle verwenden nur ungenaue Werte für diese Faktoren. Wir ermittelten zunächst die Blattlebensdauer für wichtige Vegetationstypen (418 Erhebungen weltweit). Indem wir die Vorgabewerte aus dem Lund-Potsdam-Jena-Modell (LPJ) durch die revidierten Werte ersetzten, ermittelten wir die dadurch verursachten Änderungen im simulierten Kohlenstoffkreislauf. Die Ergebnisse zeigten, dass die zusammengetragenen Beobachtungen zur Blattlebensdauer sich signifikant von den Vorgaben des LPJ-Modells unterschieden. Sowohl Produktion als auch Respiration der Vegetation der simulierten Ökosysteme zeigten mit den überarbeiteten Werten signifikante Veränderungen gegenüber den mit Vorgabewerten errechneten Vorhersagen. Von allen Variablen zeigten die ober- und unterirdischen Streuvorräte die größten

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Veränderungen (durchgängig etwa 10%). Die Vorgabewerte verursachten eine signifikante Überschätzung der terrestrischen Kohlenstoffsinke um 3% im Vergleich zu einer Simulation mit den revidierten Werten. Darüber hinaus verursachten Unsicherheiten bei den Blattlebensdauern verschiedene Unsicherheiten (5–30%) bei den simulierten Kohlenstoffflüssen und –vorräten. Genauere Daten zur Blattlebensdauer sind entscheidend für die Simulation von Vegetationsverteilung und Kohlenstoffkreislauf im Ökosystem.

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Keywords: Leaf longevity; Leaf turnover rate; Lund-Potsdam-Jena model; Ecosystem carbon cycle; Model uncertainty

Introduction

Dynamic global vegetation models (DGVMs) are indispensable tools for studying terrestrial ecosystem processes and their interactions with climate change (Prentice, Heimann, & Sitch, 2000; Wramneby, Smith, Zaehle & Sykes, 2008). Since the 1980s, the need to better understand and quantify the global behavior of terrestrial ecosystems as a major factor in earth system dynamics has driven the development of DGVMs (Sitch et al., 2003). Several of the fully integrated DGVMs, such as the Lund-Potsdam-Jena (LPJ) model and the Integrated Biosphere Simulator model (IBIS), which combine the biogeochemical and biogeographic modeling approaches have been developed (Foley et al., 1996; Sitch et al., 2003; Sato, Itoh, & Kohyama, 2007) and used widely to investigate and estimate the vegetation dynamics, biogeochemical processes, carbon balance and ecosystem responses to environmental changes on a regional or global scale (Kucharik et al., 2000; Dargaville et al., 2002; Yurova, Volodin, Agren, Chertov, & Komarov, 2010).

Nevertheless, DGVMs still contain many uncertainties in both model structures and parameters (Fisher et al., 2010; Wang et al., 2010; Yuan et al., 2012). It is well-known that DGVMs are globally parameterized models (Zaehle, Sitch, Smith, & Hatterman, 2005). However, imperfect knowledge of processes and limited observations restrict the model parameterization, and result in large model errors (Hallgren & Pitman, 2000; Snowling & Kramer, 2001). Wramneby et al. (2008) suggested that the parameter uncertainties in LPJ could lead to a shift in plant competitive balance. Zaehle et al. (2005) concluded that the uncertainty in parameters generated considerable uncertainty in global net primary production by controlling assimilation rate, plant respiration and water balance. Generally, different parameters represent the predominant influence on different processes. Jiang et al. (2012) suggested that the relative importance of parameters varied both temporally and spatially, and was shifted by climate inputs. Therefore, to assess the reliability of modeled scenarios and to identify parameters that require further development, it is necessary to examine the parameter uncertainties (White, Thornton, Running, & Nemani, 2000; Sykes, Prentice, Smith, Cramer, & Venevsky, 2001).

Leaf longevity and turnover rate are important plant traits and vary substantially among species (Chabot & Hicks, 1982; Kattge, Diaz, Lavorel, Prentice, & Leadley, 2011; Schleip, Lattanzi, & Schnyder, 2013); however, they are modeled roughly in current DGVMs. Previous studies regard leaf longevity and turnover rate as indicative of a plant's trade-off between productivity and persistence, as they determine the residence time of leaves and then constrain the circulation rate of carbon and nutrients to a certain extent (Reich, Walters, & Ellsworth, 1992; Schleip et al., 2013). Therefore, they are two critical parameters characterizing plant traits in vegetation models. Plant leaf longevity shows large differences ranging from a few weeks to more than 10 years (Reich et al., 1992; Kikuzawa, 1995). DGVMs, however, generally assumed inaccurate values of leaf longevity and turnover rate for each plant type, and previous studies have indicated substantial differences between the default values and observations (Kikuzawa & Lechowicz, 2006). To our knowledge, few studies have calibrated the parameters of leaf longevity and turnover rate for major plant types worldwide. Therefore, it is necessary to investigate the uncertainties brought about by coarsely assigned leaf longevity and turnover rate, and the corresponding impacts on model outputs.

Several studies have approached the issue of parameterization uncertainty in DGVMs (White et al., 2000; Zaehle, Sitch, Smith & Hatterman, 2005; Wramneby et al. 2008), however, few of these are related to the parameters of leaf longevity and turnover rate. In this study, we adopted the LPJ model, which is typical of DGVMs as a family of models and has been used widely to estimate global or regional carbon cycle, both with respect to its representation of structural ecosystem components (plants and soil) and ecosystem processes (Sitch et al., 2003; Zaehle et al., 2005; Bondeau et al., 2007; Yurova et al., 2010). Then, the leaf longevity and turnover parameters for each plant functional type (PFT) were revised based on numerous observational datasets. Finally, the model was run with the default and revised parameter sets, respectively. By comparing the model outputs with default and revised parameter sets, we aimed to investigate the impacts of revised leaf longevity and turnover parameters on estimates of vegetation dynamics, ecosystem production and respiration, dynamic of carbon pools and carbon balance as modeled by LPJ.

Table 1. Leaf longevity and turnover parameters for each plant functional type (PFT). TrBE: tropical broadleaved evergreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; BoNE: boreal needle-leaved evergreen forest; TrBR: tropical broadleaved rainforest; TeBS: temperate broadleaved summergreen forest; BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous. The default values of leaf longevity and turnover rate in LPJ are obtained from [Sitch et al. \(2003\)](#), and the median, 25p and 75p values correspond to the median, 25th percentile, and 75th percentile of the observed values, respectively. *N* is the number of measurements for leaf longevity (or leaf turnover rate).

PFT	Leaf longevity (year)				Leaf turnover rate (yr ⁻¹)				<i>N</i>
	Default	Median	25 p	75p	Default	Median	25 p	75p	
TrBE	2.0	1.7	1.0	2.2	0.50	0.59	1.00	0.45	108
TeNE	2.0	3.2	2.1	6.5	0.50	0.31	0.48	0.15	94
TeBE	1.0	1.3	0.9	2.1	1.00	0.77	1.11	0.43	122
BoNE	2.0	6.5	4.2	8.3	0.50	0.15	0.24	0.12	94
TrBR	0.5				1.00				–
TeBS	0.5				1.00				–
BoBS	0.5				1.00				–
TeH	1.0				1.00				–
TrH	1.0				1.00				–

Materials and methods

The Lund-Potsdam-Jena model

The Lund-Potsdam-Jena (LPJ) dynamic vegetation model integrates key ecosystem processes such as vegetation growth, dynamics, mortality, carbon allocation and soil and litter biogeochemistry ([Gerten, Schaphoff, Haberlandt, Lucht, & Sitch, 2004](#)). It is driven by monthly meteorological datasets, soil types and atmospheric carbon dioxide (CO₂) concentration. Plant functional types (PFTs) are assigned to account for the variety of plant structure and function, and nine PFTs are defined for the potential natural vegetation based on LPJ version 3 (<http://www.pik-potsdam.de>) ([Table 1](#)). Gross primary production (GPP) is calculated for each PFT, applying the coupled photosynthesis and water balance schemes ([Haxeltine and Prentice 1996](#)). Ecosystem respiration is the sum of autotrophic respiration and heterotrophic respiration, and the autotrophic respiration is derived from plant growth respiration and maintenance respiration. Heterotrophic respiration is derived from the decomposition of aboveground litterfall, belowground litter pool and soil organic matter (SOM). The net ecosystem production (NEP) is the difference between GPP and ecosystem respiration. A more detailed description of LPJ can be found in the Appendix A and [Sitch et al. \(2003\)](#).

LPJ employs an empirical relationship derived by [Reich, Walters, & Ellsworth \(1997\)](#) to relate specific leaf area (SLA, m² g C⁻¹) to leaf longevity:

$$SLA = 2.0 \times 10^{-4} \cdot \frac{e^{6.15}}{12a_{\text{leaf}}^{0.46}} \quad (1)$$

Therefore, leaf longevity (a_{leaf} , yr) is an important variable for calculating leaf area index (LAI) and foliar projective cover (FPC) successively by determining the specific leaf area

([Sitch et al., 2003](#)). The FPC, ranging from 0 to 1, is defined as the area of ground covered by foliage directly above it, and it is used to indicate vegetation dynamics.

Leaf turnover rate (f_{leaf} , yr⁻¹) is used to calculate the annual increase of leaf litter transferred from living leaves (Eq. 2), and it plays an important role in determining the canopy biomass, carbon allocation and annual litter input.

$$C_{\text{litter}} = \sum_{\text{PFT}} (C_{\text{leaf}} f_{\text{leaf}} P) \quad (2)$$

where C_{litter} is the transferred leaf litter from living leaf; C_{leaf} is the living leaf biomass; P is the stand population density.

Revised leaf longevity and turnover parameters

In herbaceous and deciduous (i.e. summergreen and rain-green) woody PFTs, plant leaves fall at the end of each growing season due to various environmental stresses. Therefore, the leaf turnover rate can be set explicitly as 1 per year. However, for evergreen PFTs, including tropical broadleaved evergreen forest (TrBE), temperate needle-leaved evergreen forest (TeNE), temperate broadleaved evergreen forest (TeBE) and boreal needle-leaved evergreen forest (BoNE), the leaf longevitys are mostly longer than 1 year. To obtain more accurate leaf longevity and turnover parameters for these four evergreen PFTs, we extracted 418 samples of leaf longevity and turnover rate from 110 publications (see Appendix A: Table A1). These reports were collected from databases including ISI Web of Knowledge, Springer Link, ScienceDirect, Journal STORage (JSTOR) and China National Knowledge Infrastructure (CNKI). Several key words, including leaf longevity, leaf turnover rate and leaf life-span were used to search the literatures at the

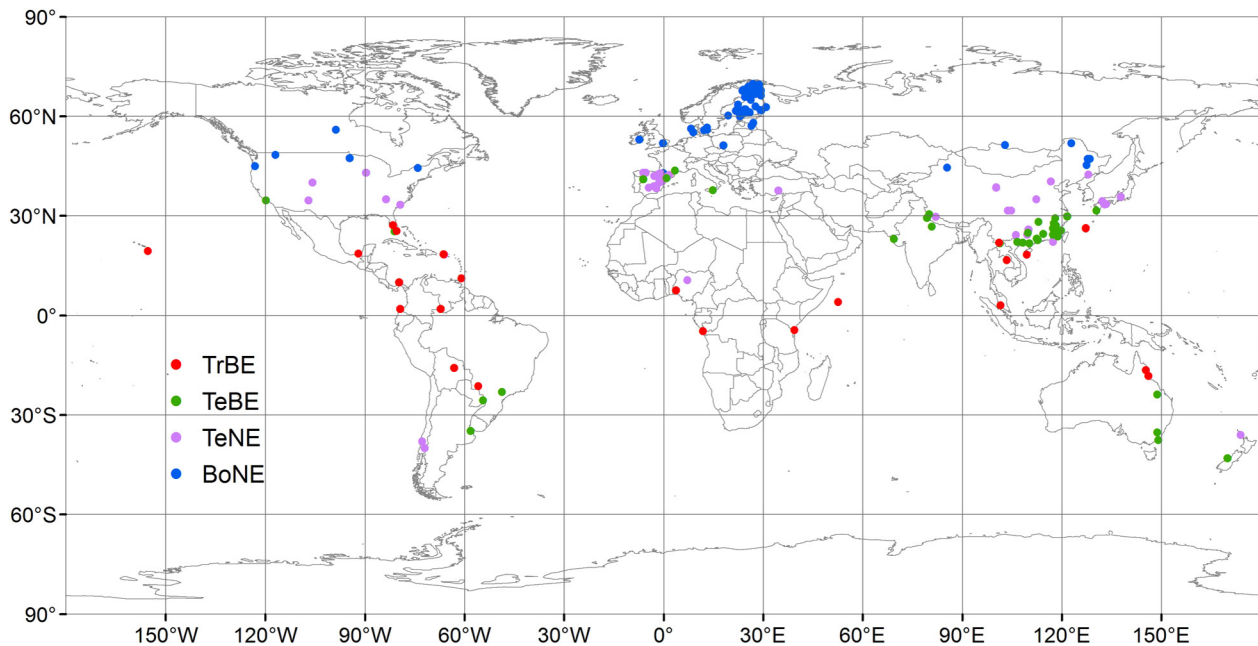


Fig. 1. Map of the observation sites for measurements of leaf longevity and turnover rate. The measurements obtained from previous studies are just for the four evergreen plant functional types in Lund-Potsdam-Jena model (LPJ). TrBE: tropical broadleaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeNE: temperate needle-leaved evergreen forest; BoNE: boreal needle-leaved evergreen forest.

above databases. The observation stations were distributed worldwide (Fig. 1). Specifically, of the 418 measurements, 108 were for TrBE, 94 were for TeNE, 122 were for TeBE and 94 were for BoNE (Table 1). The median value of measurements belonging to each PFT was regarded as the most appropriate leaf longevity, and the 25th and 75th percentile values were used to characterize the uncertainties of leaf longevity for each PFT. Leaf turnover rate is calculated as the reciprocal of leaf longevity.

Modeling and analysis

The time series of climatic data (temperature, precipitation and cloud cover) from 1979–2009 for model input were taken from the Modern Era Retrospective-Analysis (MERRA) for Research and Applications reanalysis on a 0.50° latitude \times 0.67° longitude global grid (Yuan et al., 2010). Data for the annual CO_2 concentration of the atmosphere (1979–2009) were the observed data at Hawaii, provided by the National Oceanic and Atmospheric Administration (NOAA, <ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/>) and the soil texture data set was obtained from the International Geosphere-Biosphere Programme (IGBP, <http://daac.ornl.gov/SOILS/guides/>).

Four model experiments with different parameter sets (default parameters in Sitch et al. (2003), the median, 25th percentile and 75th percentile of the revised leaf longevity) were conducted to examine the impacts of leaf longevity and turnover on carbon cycle. In all of the four experiments, the

leaf longevity and turnover rates of deciduous PFTs were all set to be the corresponding default values in LPJ. For each parameter set, the model was run for a “spin-up” period of 1000 years from the bare ground, to achieve equilibrium in terms of stable vegetation structure and carbon pools. During this phase, 31 years (1979–2009) of climate data (including temperature, precipitation and cloud cover), CO_2 data and soil texture data were repeated continuously. After the spin up period, the model was run from 1979 to 2009.

The impacts of leaf longevity and turnover parameters on ecosystem carbon cycle were examined by comparing the model outputs simulated with the original and revised parameters. We showed the changes in annual foliar projective cover (FPC), plant production, ecosystem respiration and carbon pools in each PFT-identified region (Fig. 2). The relative changes in simulated ecosystem carbon fluxes and carbon pools were calculated as:

$$\text{Relative change} = \frac{\text{Result}_{\text{revised}} - \text{Result}_{\text{default}}}{\text{Result}_{\text{default}}} \times 100\% \quad (3)$$

where the $\text{Result}_{\text{revised}}$ and $\text{Result}_{\text{default}}$ are the simulated results by LPJ with the revised and default parameters of leaf longevity, respectively. Moreover, the uncertainties in model outputs caused by the uncertainties in leaf longevity and turnover parameters were investigated by comparing the outputs simulated with the median, 25th percentile, 75th percentile and model default leaf longevity and turnover parameter sets (Table 1).

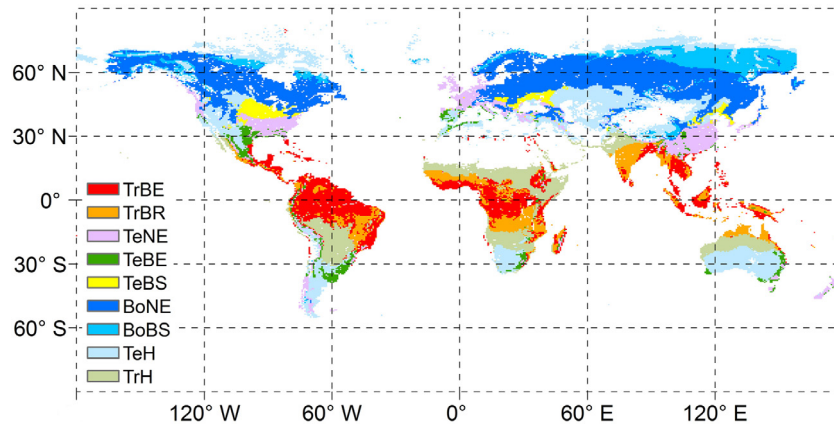


Fig. 2. Representation of the plant functional types simulated by LPJ with the default leaf longevity and turnover rates. A grid square would belong to the plant functional type (PFT) owning the largest mean foliar projective cover (FPC) for 1979–2009. TrBE: tropical broadleaved evergreen forest; TrBR: tropical broadleaved raingreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeBS: temperate broadleaved summergreen forest; BoNE: boreal needle-leaved evergreen forest. BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous.

Results

Leaf longevity and turnover rate

From all 418 field measurements, leaf longevity and turnover rate were calculated for four evergreen forest types. The results showed significant differences in leaf longevity at the four evergreen PFTs. The shortest leaf longevity was found in temperate broadleaved evergreen forests (TeBE), with a median value of 1.3 years, an intermediate longevity was found in tropical broadleaved evergreen forests (TrBE, 1.7 years) and temperate needle-leaved evergreen forests (TeNE, 3.2 years), and these were significantly lower than the leaf longevity in boreal needle-leaved evergreen forests (BoNE, 6.5 years) (Table 1). Within each of the four PFTs, the leaf longevities also varied strikingly. For example, in BoNE, the longest observed leaf longevity was almost 12 years, which was almost six times of the shortest (see Appendix A: Table A1).

Furthermore, *t*-test suggested that the default leaf longevities in LPJ were significantly different ($p < 0.01$) from the observations at all four of the PFTs. The default leaf longevity of TrBE (2 years) was significantly larger than the observations. However, the default value for TeBE (1 year) was overall smaller than the observations. In both TeNE and BoNE, the default values were even smaller than the 25th percentile of observations. In particular, the observed leaf longevity of BoNE (6.5 years) was more than three times of the default value (2 years).

Impacts of leaf longevity and turnover rate on vegetation dynamics

We examined the impacts of leaf longevity and turnover rate on plant foliar projective cover (FPC) by driving the

LPJ model with the default and revised (median) parameter values, respectively. The revised parameters caused various changes in FPC simulation, with low decreases of FPC (mean value, -0.006) in tropical broadleaved evergreen forests (TrBE) (Fig. 3a), moderate decreases (mean value, -0.016) in temperate needle-leaved evergreen forests (TeNE) (Fig. 3d), relatively large decreases (mean value, -0.032) in boreal needle-leaved evergreen forests (BoNE) (Fig. 3g) and a mean 0.005 increase in temperate broadleaved evergreen forests (TeBE) (Fig. 3e). The changes in FPC of the deciduous and herbaceous PFTs were mostly converse to those of the coexisting evergreen PFTs.

The FPC changes of evergreen PFTs generally showed significantly negative correlations with those of the coexisting deciduous or herbaceous PFTs (Table 2). The changes in FPC of TrBE showed significantly negative correlations to TrBR ($r = -0.83$) and TrH ($r = -0.66$). The changes in FPC of TeNE were negatively correlated with TeH ($r = -0.18$), TeBS ($r = -0.37$) and TeBE ($r = -0.25$). For TeBE, the changes in FPC were negatively correlated with the changes for TeH ($r = -0.88$). The changes in FPC of BoNE also showed significantly negative correlations to the coexistent PFTs.

Impacts of leaf longevity and turnover rate on ecosystem carbon fluxes

Our study indicated that the revised (median) leaf longevity and turnover rates caused significant changes in ecosystem carbon fluxes in most PFTs (Fig. 4). Except for tropical broadleaved deciduous forests (TrBR) and temperate herbaceous (TeH), the revised parameters caused significant decreases (smaller than 1%) in gross primary production (GPP) in the remaining PFTs (Fig. 4a). The changes in net primary production (NPP) were also significantly decreased in most PFTs, and BoNE presented the largest decrease of

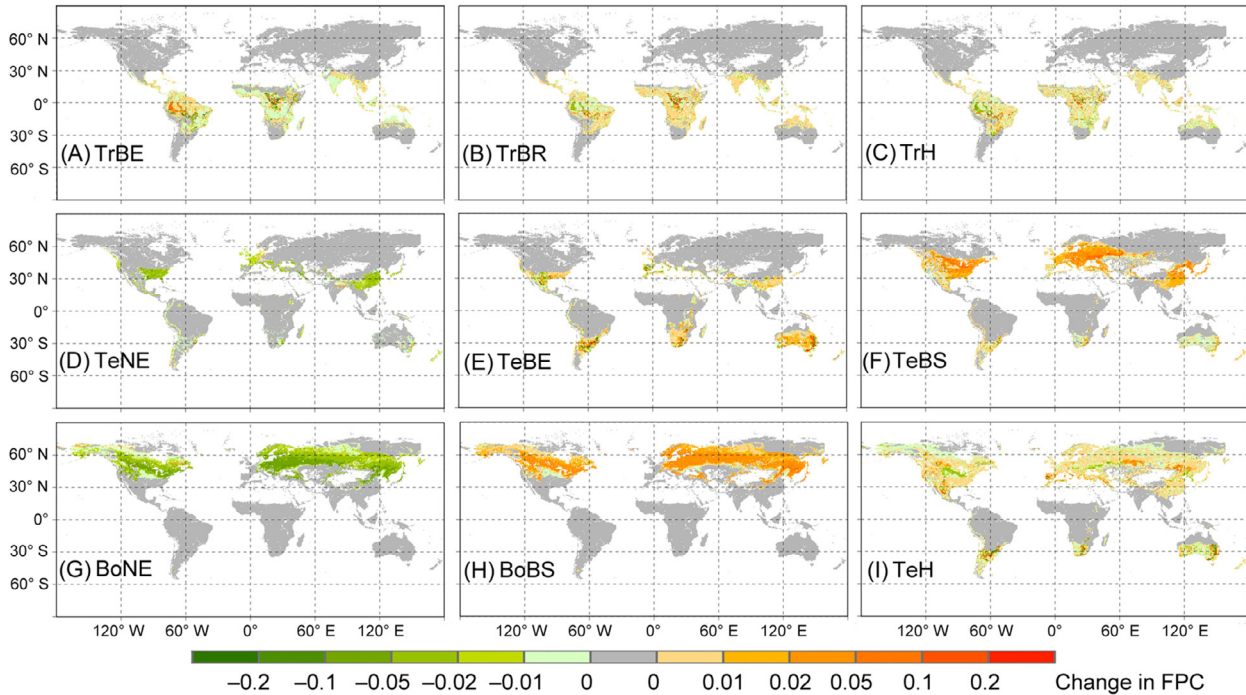


Fig. 3. Maps of the changes in mean 1979–2009 foliage projective cover (FPC) between simulations with the revised (median) and default leaf longevity and turnover parameter. Change = $FPC_{\text{revised}} - FPC_{\text{default}}$. TrBE: tropical broadleaved evergreen forest; TrBR: tropical broadleaved raingreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeBS: temperate broadleaved summergreen forest; BoNE: boreal needle-leaved evergreen forest. BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous.

Table 2. Correlation of the changes in foliage projective cover for each PFT between simulations with default and median parameter sets. *r*: Pearson correlation coefficient; *N*: number of grids with both of the corresponding PFTs; TrBE: tropical broadleaved evergreen forest; TrBR: tropical broadleaved raingreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeBS: temperate broadleaved summergreen forest; BoNE: boreal needle-leaved evergreen forest. BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous; ** Significant at $p < 0.01$.

PFT		TrBE	TrBR	TeNE	TeBE	TeBS	BoNE	BoBS	TeH	TrH
TrBE	<i>r</i>	1	-0.83**	-0.12**	-0.19**	-0.20**	–	–	0.10	-0.66**
	<i>N</i>	9703	9402	1465	1997	170	0	0	219	9519
TeNE	<i>r</i>	-0.12**	-0.20**	1	-0.25**	-0.37**	-0.34**	-0.16**	-0.18**	-0.01
	<i>N</i>	1465	1629	7375	5420	5590	442	455	5766	1789
TeBE	<i>r</i>	-0.19**	-0.19**	-0.25**	1	-0.37**	–	–	-0.88**	-0.32**
	<i>N</i>	1997	2222	5420	7708	5468	0	0	5642	2356
BoNE	<i>r</i>	–	–	-0.34**	–	-0.51**	1	-0.76**	-0.38**	–
	<i>N</i>	0	0	442	0	4958	12896	12827	12881	0

6% (Fig. 4b). On the contrary, TrBE showed a significant increase. With the observed parameters, TrBE, TrBR and TrH presented significant decreases in autotrophic respiration. The other PFTs except for TeBS presented significant increases. The largest increase (4%) occurred in BoNE (Fig. 4d). The changes in heterotrophic respiration were opposite to the changes in autotrophic respiration. BoNE showed the largest decrease of approximately 6% (Fig. 4e). Ecosystem respiration which was the sum of autotrophic and heterotrophic respiration, showed relatively small changes (within 1%, Fig. 4f). Net ecosystem production (NEP), calculated as the difference between GPP and ecosystem

respiration, showed no significant changes at TrBE, TrBR, TeBS and the, but significant decreases at all of the other PFTs. Globally, the revised parameters induced a significant decrease of 3% in terrestrial NEP (Fig. 4c).

Impacts of leaf longevity and turnover rate on carbon pools

Leaf longevity and turnover rates changed vegetation biomass and carbon pools strongly (Fig. 5). In TrBE, TeBS

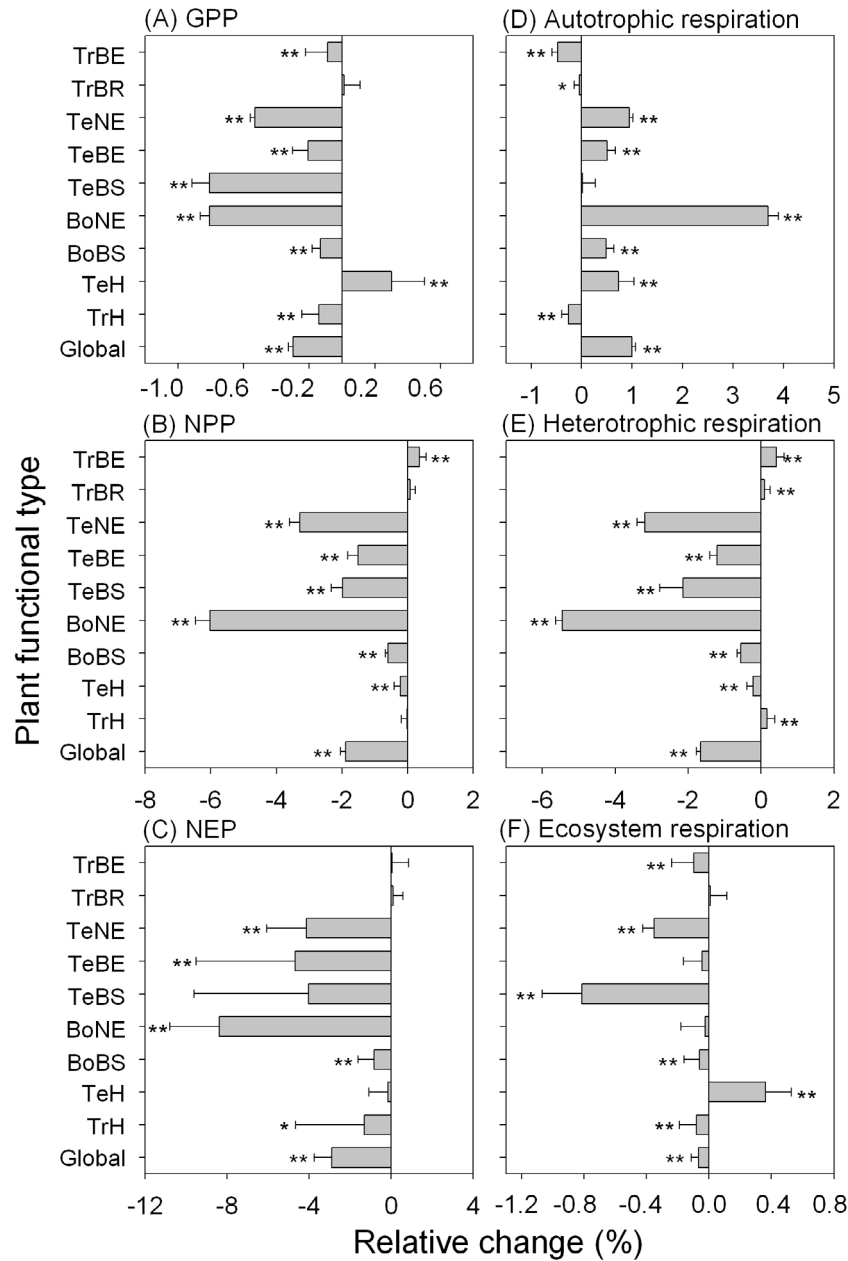


Fig. 4. Relative changes in total ecosystem production (GPP: gross primary production, NPP: net primary production, NEP: net ecosystem production) and respiration (autotrophic respiration, heterotrophic respiration, ecosystem respiration) simulated with the revised (median) and default leaf longevity and turnover parameters for each plant functional type. The error bar shows the standard deviation. ** very significant change ($p < 0.01$); * significant change ($p < 0.05$). TrBE: tropical broadleaved evergreen forest; TrBR: tropical broadleaved raingreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeBS: temperate broadleaved summergreen forest; BoNE: boreal needle-leaved evergreen forest. BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous.

and TeH, the revised parameters (median) caused significant increases in vegetation biomass. In the remaining PFTs, significant decreases in vegetation biomass occurred with the revised parameters (Fig. 5a). Use of the revised parameters induced opposite changes in the aboveground and belowground litter pools across all PFTs (Fig. 5b and c). Globally, the revised parameters induced an 8% decrease in

aboveground litter pool and 10.6% increase in belowground litter pool. In BoNE, the changes in aboveground and belowground litter pool could be a 16% decrease and 30% increase, respectively. Use of the revised parameters induced significant increases in the soil organic material (SOM) pools in TrBE and TrH, however significant decreases for the remaining PFTs (Fig. 5d).

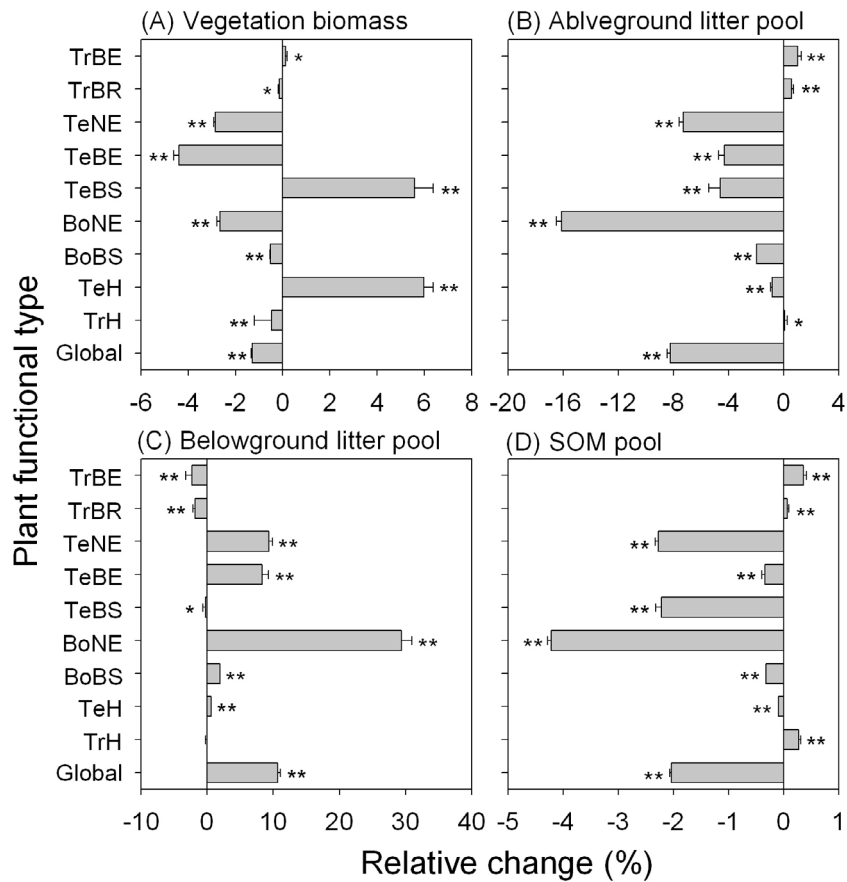


Fig. 5. Changes in total carbon pools simulated with the revised (median) and default leaf longevity and turnover parameters for each plant functional type. SOM is soil organic matter. The error bar shows the standard deviation. ** very significant change ($p < 0.01$); * significant change ($p < 0.05$). TrBE: tropical broadleaved evergreen forest; TrBR: tropical broadleaved raingreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeBS: temperate broadleaved summergreen forest; BoNE: boreal needle-leaved evergreen forest. BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous.

Uncertainties in model outputs

We examined the uncertainties in model outputs sourced from the uncertainties in leaf longevity and turnover rates by driving LPJ with the median, 25th percentile and 75th percentile values for leaf longevity parameters (Table 1), respectively. These results suggested that the uncertainties in leaf longevity and turnover rates caused certain uncertainties in ecosystem carbon fluxes and carbon pools in all plant types (Fig. 6). The resulting uncertainties in ecosystem production (GPP, NPP and NEP) and respiration were mostly less than 10%, which were smaller than the resulting uncertainties in vegetation biomass and carbon pools. In TeBE, the uncertainties in vegetation biomass exceeded 30% (Fig. 6g). In TeNE, the uncertainties in aboveground and belowground litter pools were greater than 10% (Fig. 6h) and 25% (Fig. 6i), respectively. Moreover, the uncertainties in leaf longevity and turnover rates generally induced larger uncertainties for evergreen plant types than for the remaining plant types (Fig. 6).

Discussion

Leaf longevity and turnover rate have been used by LPJ to calculate several key processes of ecosystem carbon cycle. Many previous studies have reported significant correlations between leaf longevity and many other leaf structural and physiological properties such as leaf photosynthetic assimilation rate, leaf nitrogen and specific leaf area (SLA) (Wright, Thornton, Running, & Nemani, 2000; Wright et al., 2004; Reich, Wright, & Lusk, 2007). LPJ employed an empirical relationship derived by Reich et al. (1997) relating SLA to leaf longevity (Eq. 1). Because SLA was used to calculate the leaf area index (LAI) and foliage projective cover (FPC), leaf longevity would further determine the vegetation dynamics, plant photosynthesis and respiration (Koike, 1987; Matsuki and Koike 2006). The leaf turnover rate in LPJ was used to calculate the annual litter input, as well as to determine the size of the canopy biomass, the substrate of heterotrophic respiration (Hikosaka, 2005). Overall, leaf longevity and turnover rate are involved in many key variables and processes in LPJ.

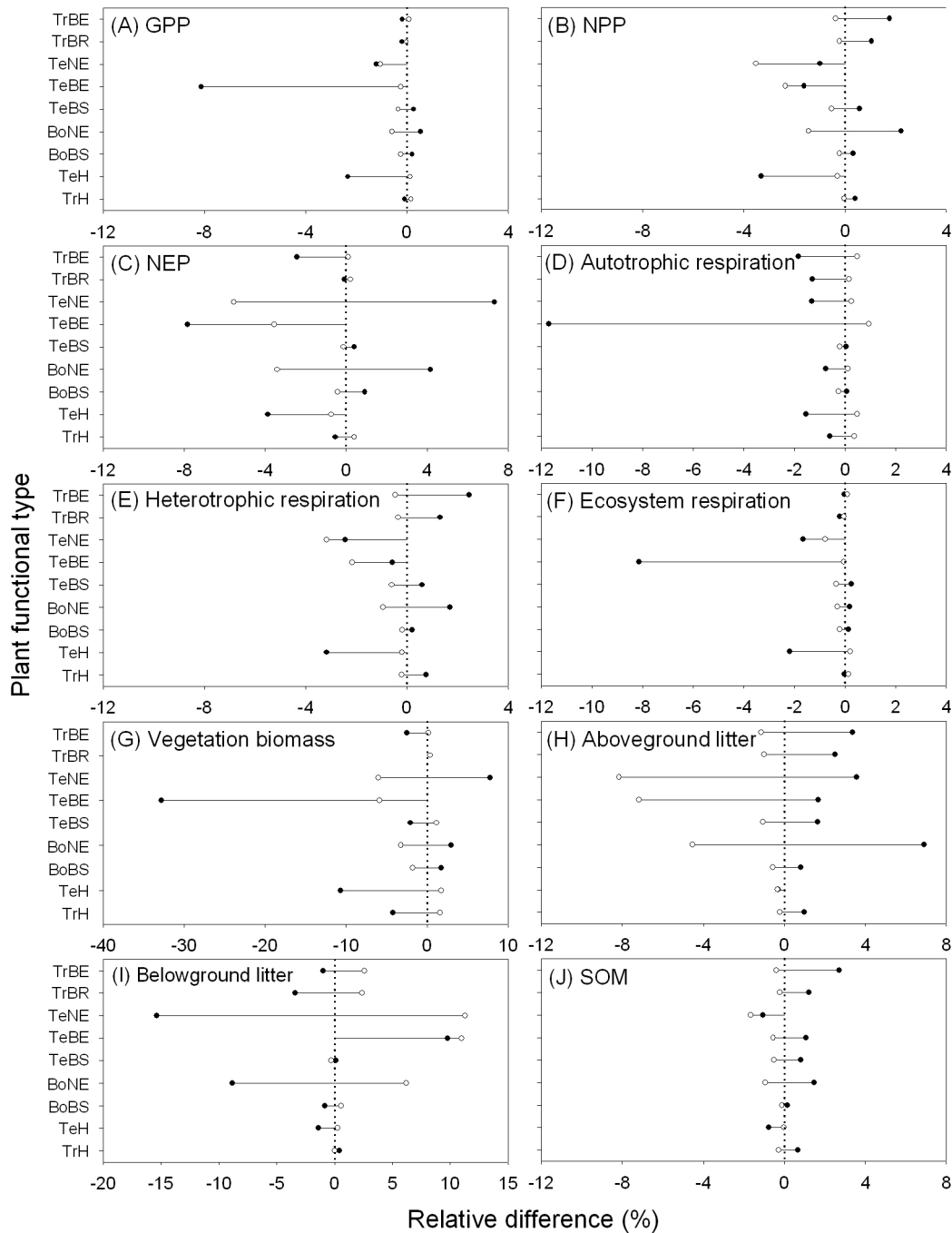


Fig. 6. Uncertainties in model outputs for simulations with different sets of leaf longevity and turnover parameters. Open circle denotes the relative change between simulations with the 25th percentile and median parameter sets. Solid circle denotes the relative change between simulations with the 75th percentile and median parameter set. The length of the line (mostly as the difference between open and solid circles) shows the degree of uncertainty. TrBE: tropical broadleaved evergreen forest; TrBR: tropical broadleaved raingreen forest; TeNE: temperate needle-leaved evergreen forest; TeBE: temperate broadleaved evergreen forest; TeBS: temperate broadleaved summergreen forest; BoNE: boreal needle-leaved evergreen forest. BoBS: boreal broadleaved summergreen forest; TeH: temperate herbaceous; TrH: tropical herbaceous.

Existing vegetation models usually assumed inaccurate leaf longevity and turnover rates for each PFT (Sitch et al., 2003; Kucharik et al., 2006). White et al. (2000) reported that the specified leaf longevity in BIOME-BGC showed large discrepancies with the observed values in the United States. Similarly, our study also indicated significant

differences between the observed and default leaf longevity for all four of the evergreen PFTs. The observed leaf longevity of BoNE was even greater than three times of the default value. Therefore, the significant errors and uncertainties in leaf longevity and turnover rates may result in substantial and uncertain estimations of ecosystem carbon cycle.

Our results suggest that using the revised (median) leaf longevity and turnover rates caused various changes in projected vegetation distributions worldwide (Fig. 2). In this way, studies adopted the default parameters may have simulated an inaccurate vegetation distributions, especially in boreal areas (Sitch et al., 2003; Lucht, Schaphoff, Erbrect, Heyder, & Cramer, 2006). Generally, longer leaf longevity means smaller specific leaf area (SLA) (Eq. 1), and thus lower leaf area index (LAI) and FPC at a certain canopy biomass. Therefore, the substantial increases in leaf longevity of BoNE (from 2 to 6.5 years) and TeNE (from 2 to 3.2 years) result in significant decreases in FPC. However, because LPJ allows for multiple PFTs growing at each location, the FPC of a certain PFT is also impacted by the coexisting PFTs. For example, the increased FPC of TeBE is mostly induced by the reduced PFC of TeNE. Moreover, the total FPC in many regions is generally maintained at 1, and the changes in FPC of evergreen PFTs are mostly offset by those of the coexisting deciduous or herbaceous PFTs. Successful coexistence of multiple PFTs can buffer the changes in ecosystem carbon cycles to the revised parameters (Fisher et al., 2010).

The default leaf longevity and turnover rates induced significant bias in simulated ecosystem carbon fluxes and carbon pools, and may misestimate the terrestrial carbon budget. In LPJ, the key biogeochemical processes for carbon cycle involve photosynthesis (Farquhar, von Caemmerer, & Berry, 1980; Collatz, Ball, Grivet, & Berry, 1991), plant autotrophic respiration (Ryan & Law, 2005) and heterotrophic respiration (Randerson, Chapin, Harden, Neff, & Harmon, 2002). Leaf longevity and turnover rate can significantly affect these processes (Sitch et al., 2003; Schleip et al., 2013). Our results indicated that use of the revised (median) parameters caused a significant decrease in net ecosystem production (NEP) of approximately 3%. Because NEP is defined as the net carbon assimilation by an ecosystem and indicates the regional carbon budget (Randerson et al., 2002), previous studies, which used the LPJ with default parameters of leaf longevity and turnover rate to predict future ecosystem carbon cycle, are likely to overestimate global carbon sink effect of terrestrial ecosystems (Schaphoff et al., 2006).

Compared with vegetation photosynthesis and respiration, the revised leaf longevity and turnover rates have induced larger changes in carbon pools. As mentioned above, leaf longevity and turnover rate are involved in many key processes of the carbon cycle. For example, longer leaf longevity means a lower leaf turnover rate, which leads to smaller amounts of standing leaves transformed into the aboveground litter pool, and the standing stock of aboveground litter will be reduced (Eq. 2). This is the main reason why the aboveground litter pool in BoNE decreased drastically with increasing leaf longevity. Furthermore, soil carbon pools are the substrates of soil respiration. In boreal areas, using the observed leaf longevity and turnover rates caused a decrease of approximately 16% in the aboveground litter pools and an increase of about 30% in the belowground litter pools. The changed carbon pools would then alter the magnitude

and composition of soil respiration, which are regarded as important factors in forest ecosystem ecology and soil science (Bond-Lamberty, Wang, & Gower, 2004, Del Grosso et al., 2005).

Another point which should be noticed is that the neutralization of biases in intermediate variables might result in reasonable model output. For example, in BoNE, the revised parameters induced an increase of 4% in autotrophic respiration (Fig. 4d) however a similar level of decrease in heterotrophic respiration (Fig. 4e). Therefore, the ecosystem respiration which is the sum of autotrophic and heterotrophic respiration only showed an insignificant change (Fig. 4f). Moreover, the revised parameters also induced large but opposite changes in the aboveground and belowground litter pools (Fig. 5b and c), which have been regarded as the two most important substrates to heterotrophic respiration (Sulzman, Brant, Bowden, & Lajtha, 2005). Therefore, heterotrophic respiration has already been calculated based on substrates with substantial biases. Overall, the offsets of many biases have induced the insignificant biases in ecosystem respiration.

A previous study suggested that model parameters, each with its intrinsic uncertainty range, potentially widen the overall uncertainty of model outputs (Wramneby et al., 2008). Leaf longevity and turnover rate, which are determined by the physiological characteristics and growth environments of the plant, generally showed considerable uncertainties (Chabot and Hicks 1982; Escudero and del Arco 1987; van Ommen Kloeke, Douma, Ordoñez, Reich, & van Bodegom, 2012). Our results indicated that the uncertainties in leaf longevity and turnover rates induced significant uncertainties in simulated carbon cycles. Carbon pools showed the largest uncertainties associated with leaf longevity and turnover rates. Most current DGVMs condense plant species with different leaf longevity and turnover rates to a plant functional type. An individual- and trait-based redefinition of the plant types can represent plants' traits (including leaf longevity and turnover rate) at different geographical locations more accurately, and will be helpful to diminish the related uncertainties in model outputs (Sakschewski et al., 2015).

Although previous studies suggested that LPJ with the default values of leaf longevity and turnover rate is able to reproduce the observed patterns of vegetation distribution as well as ecosystem carbon budget well (Morales et al., 2005; Mahecha et al., 2010), the adjustments of the other parameters in LPJ may have covered up the biases caused by the erroneous parameters of leaf longevity and turnover. As the results of the present study, the erroneous leaf longevity and turnover rates can induce large biases in the intermediate variables of LPJ (e.g. above- and belowground litter pools). In order to ensure the simulated ecosystem carbon budget agree well with observations, the adjustments of the other parameters are necessary. However, these adjustments may result in reasonable ecosystem carbon budgets with incorrect intermediate variables and processes. An excellent DGVM should be able to reproduce not only the final vegetation

distribution and carbon budget but also the intermediate variables and processes.

Finally, there are still some shortcomings in present study should be noticed and overcome in future work. First, the measurements of leaf longevity and turnover rate are mostly obtained from Europe and China (Fig. 1), therefore the values of leaf longevity and turnover rate used in the present study may contain certain biases compared with global mean values. Second, many other critical parameters (e.g. turnover rates of root, sapwood or litter) in LPJ also contain large uncertainties (Zaehle et al., 2005; Wramneby et al., 2008). Uncertainties in these parameters can induce considerable biases in model outputs, and then disturb the contribution of uncertainties in leaf longevity and turnover rate to the final model biases. Finally, LPJ adopts many empirical or simplified algorithms to represent different carbon cycle processes (Sitch et al., 2003). The uncertainties in algorithms and structure of LPJ can also impact the uncertainties in model output caused by leaf longevity and turnover rate. Overall, more works are necessary to diminish the uncertainties in both model parameters and algorithms.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.01.006>.

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