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Research

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Sensitivity Analysis of Biome-BGCMuSo for Gross and Net Primary Productivity of Typical Forests in China

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Abstract

Background: Process-based models are widely used to simulate forest productivity, but complex parameterization and calibration challenge the application and development of these models. Sensitivity analysis of numerous parameters is an essential step in model calibration and carbon flux simulation. However, parameters are not dependent on each other, and the results of sensitivity analysis usually vary due to different forest types and regions. Hence, global and representative sensitivity analysis would provide reliable information for simple calibration.

Methods: To determine the contributions of input parameters to gross primary productivity (GPP) and net primary productivity (NPP), regression analysis and extended Fourier amplitude sensitivity testing (EFAST) were conducted for Biome-BGCMuSo to calculate the sensitivity index of the parameters at four observation sites under climate gradient from ChinaFLUX.

Results: Generally, GPP and NPP were highly sensitive to C:N_leaf (C:N of leaves), $W_{int}$ (canopy water interception coefficient), $k$ (canopy light extinction coefficient), FLNR (fraction of leaf N in Rubisco), $MR_{per}$ (maintenance respiration in kg C/day per kg of tissue N), $VPD_r$ (vapor pressure deficit complete conductance reduction), and $SLA_1$ (canopy average specific leaf area in phenological phase 1) at all observation sites. Various sensitive parameters occurred at four observation sites within different climate zones. GPP and NPP were particularly sensitive to FLNR, $SLA_1$ and $W_{int}$, and C:N_leaf in temperate, alpine and subtropical zones, respectively.

Conclusions: The results indicated that sensitivity parameters of China's forest ecosystems change with climate gradient. We found that parameter calibration should be performed according to plant functional type (PFT), and more attention needs to be paid to the differences in climate and environment. These findings contribute to determining the target parameters in field experiments and model calibration.

Keywords: Sensitivity Analysis; Biome-BGCMuSo; productivity; regression analysis; EFAST
1. Introduction

Forests can remove approximately one quarter of the carbon dioxide emitted by fossil fuels and industry, becoming one of the most important nature-based solutions to climate change (Seidl et al. 2017; FAO 2020; Cook-Patton et al. 2020). Accurate simulation of forest carbon fluxes, for example, gross primary productivity (GPP) and net primary productivity (NPP), is an important element of the terrestrial ecosystem carbon cycle and global climate change research. Process-based simulation (PBS) models (e.g., Biome-BGC-MuSo, Community Land Model) take atmosphere-vegetation-soil as a continuous and dynamic system to establish material and energy exchange modules (Pan et al. 2014; Sun et al. 2017) and can describe the main processes of forest ecosystems (e.g., carbon, nitrogen, and water flux dynamics). Recently, the development of PBS models has provided potential opportunities in terms of terrestrial ecosystem carbon and water cycles and their responses to global climate change (Zaehle et al. 2005; Wang et al. 2011; Li et al. 2020). The running of PBS models relies on conventional ground data, including climatology, meteorology, and vegetation ecophysiological parameters, which results in uncertainties in model outputs due to insufficient prior knowledge of site-specific input parameters (Zhou et al. 2021). Therefore, model calibration by identifying the most influential parameters is necessary for the accurate simulation of carbon and water fluxes.

Sensitivity analysis quantifies how changes in model outputs are attributed to variations in input parameters, and it is widely used in uncertainty assessment, model calibration and diagnostic evaluation and leading control analysis of PBS models (Pianosi et al. 2016). Raj et al. (2014) performed variance-based sensitivity analysis for NPP and GPP from the Biome-BGC model in Douglas-fir forests, and the findings demonstrated that GPP and NPP were particularly sensitive to the C:N of fine roots and leaves related to the development of the leaf area index. Miyauchi et al. (2019) estimated the carbon density of biomass pools in Eucommia ulmoides plantations on the Loess Plateau and believed that the allocation parameters, along with specific leaf area (SLA) and maximum stomatal conductance ($g_{\text{max}}$), strongly affected aboveground woody (AC) and leaf carbon (LC) density in a sensitivity analysis. Dagon et al. (2020) developed a machine learning method to proceed with the sensitivity and uncertainty of the community land model parameters, which provided an effective framework in model calibration. The results of site-level sensitivity analysis may not be transferable to other regions owing to the climate, soil, and vegetation types. Comprehensive sensitivity analysis of multiple sites and various methods from PBS models are indispensable to understand the expressions of sensitive parameters among vegetation function types and regions.

Biome-BGC-MuSo is a newly developed PBS model from Biome-BGC to simulate carbon, nitrogen, and water fluxes, which improves the phenology, multilayer soil, and management modules (Hidy et al. 2016, 2021). It requires about 82 ecophysiological parameters to characterize the vegetation processes at the site and over large areas. White et al. (2000) performed parameterization and sensitivity analysis on most ecophysiological parameters of BIOME-BGC, and the results provide a valuable reference for the parameterization and calibration of the model (Turner et al. 2005; Shields and Tague 2015; Miyauchi et al. 2019; Neumann et al. 2020). However, the results ignored the parameter differences in different climate zones and mainly analyzed PFT variability. In addition, with the improvement of the model, the influence
of module coupling on the parameters is unknown. Previous studies suggested that sensitivity analysis results may vary according to specific species and regions (White et al. 2000; Tatarinov and Cienciala 2006; Raj et al. 2014; Miyauchi et al. 2019). This may even influence the calibration procedure of Biome-BGCMuSo for specific species under different environmental and site conditions.

In this paper, we applied regression analysis and EFAST to identify the sensitive parameters of the Biome-BGCMuSo model for GPP and NPP at four sites in China. Our goals are to determine the sensitivity index of input parameters for GPP and NPP and to use this knowledge to gain insight into the capability of the Biome-BGCMuSo model. We aimed to solve the following questions: (1) What are the sensitive parameters for GPP and NPP of different plant functional types (PFTs) in China? (2) How does the response of forest productivity to sensitive parameters change with environmental gradients? This would provide us with informative parameters for further calibration steps and could be extended to the regional scale.

2. Materials and Methods

2.1. Observation sites

Four observation sites were selected in this study, which were included in ChinaFLUX (Yu et al. 2006, 2016). These sites cover a large range of latitudes (between 42°N and 21°N), climate zones and forest species from North to South China (Figure 1). The forest species follow specific latitude patterns, ranging from needle forest and deciduous broad-leaved forests (DBF) in the north to evergreen broad-leaved forest (EBF) and evergreen needle-leaved forests (ENF) in the south as well as shrubs in the alpine climate zone on the edge of the Qinghai-Tibetan Plateau (Table 1). Eddy covariance (EC) systems were used to assess the accuracy of Biome-BGCMuSo in simulating GPP and NPP. The observation sites use an open-circuit vorticity correlation system to carry out flux observations and simultaneous gradient observations of conventional meteorological elements. From the ChinaFLUX data, we obtained daily GEE and NEE during the 2003–2010 period for the eddy covariance (EC)-based carbon flux towers at the four observation sites (Zhang et al. 2020; Dai et al. 2020; Wu et al. 2020; Li et al. 2021). The acquired data are based on the ChinaFLUX technology system to complete standardized quality control and data processing. The daily GPP and NPP values were calculated by inverse operation of GEE and NEE.
The Changbaishan forest site (CBS) is in Jilin Province, with geographic coordinates of 128°05'E and 42°24'N and an altitude of 738 m. The CBS has a temperate continental climate with significant mid-latitude mountain climate characteristics (Chu et al. 2018). It is dry and windy in spring, hot and rainy in summer, and dry and cold in winter, with an average annual temperature of 3.6 °C and an average annual rainfall of 713 mm. The annual sunshine duration is 2271~2503 hours. The main vegetation is *Pinus koraiensis* Sieb. et Zucc. and broad-leaved mixed forest on the surface beneath the flux tower. The main tree species are *Pinus koraiensis* Sieb. et Zucc., *Tilia tuan* Szyszyl., *Quercus mongolica* Fisch. ex Ledeb., *Fraxinus mandshurica* Rupr., and *Acer pictum* Thunb. ex Murray, with an average tree height of 26 m (Bai et al. 2014). The average ratio of *Pinus koraiensis* Sieb. et Zucc. to broad-leaved forest at the CBS site from 2005 to 2010 was 1:9. The soil type is upland dark brown forest soil. The surface organic matter content is approximately 10%. The nitrogen content is approximately 0.3%. In addition, the C:N ratio is approximately 20%, and the clay content is 31% (Sun et al. 2019).

The Haibei grassland site (HB) is in the northeastern part of the Qinghai-Tibetan Plateau. We chose the shrub ecological type at the HB site, with geographic coordinates of 101°19'E and 37°39'N and an altitude of 3358 m. HB has alpine continental climate characteristics. Restricted by high altitude conditions, the temperature is extremely low. The annual average temperature is -1.2 °C, the average temperature of the hottest month (July) is 10.4 °C, and the average temperature of the coldest month (January) is -14.4 °C. The average annual precipitation is 535.2 mm, and the precipitation during the warm season (from May
to September) during the plant growth period is 437.5 mm, accounting for 82% of the annual precipitation (Li et al. 2019). The annual sunshine duration is 2451.7 h. The dominant and associated species are *Potentilla fruticosa* L. and *Kobresia humilis* Serg., *Festuca ovina* L., and *Stipa aliena* Keng.. At the end of the plant growth period (September), the vegetation coverage can reach approximately 85% (Li et al. 2016). The height of *Potentilla fruticosa* L. in the upper canopy is approximately 0.6 m, and the average height of the lower herbaceous plants is approximately 0.18 m (Fu et al. 2006). The main soil type is alpine shrub meadow soil. The organic matter content of the 0-40 cm soil layer is 11.94%, and the soil nitrogen content is 0.62% (Hu et al. 2019).

The Qianyanzhou forest site (QYZ) is in Jiangxi Province, with geographic coordinates of 115°03′E and 26°44′N. QYZ has typical mid-subtropical monsoon climate characteristics, with a dry winter season and heavy summer rainfall (Yu et al. 2008). The annual average temperature is 17.9°C, the annual average precipitation is 1542.4 mm, the annual evaporation is 1110.3 mm, and the average annual relative humidity is 84%. Most of the existing forest stands are coniferous forests planted in approximately 1985, and the main tree species are *Pinus massoniana* Lamb., *Pinus elliottii* Englem., *Cunninghamia lanceolata* (Lamb.) Hook. and *Schima superba* Gardn. et Champ.; evergreen vegetation covers 76% of the total land area (He et al. 2019). The weathering layer in the QYZ is generally 30 to 50 cm thick, and the main soil type is typical red earth (Li et al. 2007).

The Dinghushan forest site (DHS) is in Guangdong Province, with geographic coordinates of 112°34′3.8″E and 23°10′N. The altitude is 300 m. DHS in the south subtropical climate zone, with obvious dry and wet seasons. The average annual temperature is 20.9 °C, the average temperature in July is 28.1 °C, and the average temperature in January is 12.0 °C. The average annual precipitation is 1956 mm, and the average annual relative humidity is 82%. The main dominant tree species are *Schima superba* Gardn. et Champ., *Pinus massoniana* Lamb. and *Castanea henryi* (Skam) Rehd. et Wils. (He et al. 2020). The average ratio of EBF to ENF at the DHS site from 2005 to 2010 was 4:6. The soil type is latosolic red soil, and the organic content of the surface layer ranges from 2.94% to 4.27% (Zhang et al. 2019).

**Table 1 Site descriptions**

<table>
<thead>
<tr>
<th>Sites</th>
<th>CBS</th>
<th>HB</th>
<th>QYZ</th>
<th>DHS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>128°05′E, 42°24′N</td>
<td>101°19′E, 37°39′N</td>
<td>115°03′E, 26°44′N</td>
<td>112°32′E, 23°10′N</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>738</td>
<td>3358</td>
<td>102</td>
<td>300</td>
</tr>
<tr>
<td>Climate zone</td>
<td>Temperate</td>
<td>Alpine</td>
<td>Mid-subtropical</td>
<td>Southern subtropical</td>
</tr>
<tr>
<td>Mean annual Temperature (°C)</td>
<td>3.6</td>
<td>-1.2</td>
<td>17.9</td>
<td>20.9</td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>713</td>
<td>535.2</td>
<td>1542.4</td>
<td>1956</td>
</tr>
<tr>
<td>PFTs</td>
<td>DBF &amp; ENF</td>
<td>Shrub &amp; Grass</td>
<td>ENF</td>
<td>EBF &amp; ENF</td>
</tr>
</tbody>
</table>
Canopy height (m) 26 0.6 12 20

Predominant species

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinus koraiensis</td>
<td>Sieb. et Zucc.,</td>
</tr>
<tr>
<td>Tilia tuan</td>
<td>Szyszyl.,</td>
</tr>
<tr>
<td>Quercus mongolica</td>
<td>Serg.,</td>
</tr>
<tr>
<td>Potentilla fruticose L.,</td>
<td>Festuca ovina L.,</td>
</tr>
<tr>
<td>Pinus massoniana</td>
<td>Lamb., Pinus elliottii Englem.,</td>
</tr>
<tr>
<td>Schima superba</td>
<td>Gardn. et Champ.,</td>
</tr>
<tr>
<td>Pinus massoniana</td>
<td>Lamb.,</td>
</tr>
<tr>
<td>Castanea henryi (Skam) Rehd. et Wils</td>
<td>(Lamb.) Hook.</td>
</tr>
</tbody>
</table>

2.2. Biome-BGCMuSo model

For this work, we used the latest version of Biome-BGCMuSo (V6.1), which was released by the research group of Prof. Zoltán Barcza at the Meteorology Department of Eötvös Lorand University (Hidy et al. 2021). Compared to Biome-BGC, Biome-BGCMuSo is mainly characterized by a multilayer soil module, drought-related plant senescence module, phenology module, and management module (e.g., cropland mowing, grazing, fertilization, harvest and forest thinning). Biome-BGCMuSo also introduced new input variables (for example, measured drain coefficient, hydraulic coefficient, ratio of dry matter and carbon content) and new output parameter variables (cumulative evaporation and transpiration).

The carbon flux module, phenology module and soil flux module are the three most important modules in Biome-BGCMuSo. In the carbon flux module, the photosynthesis program of Farquhar (1980) and the enzyme kinetic model based on Woodrow and Berry (1988) are used to calculate the GPP of the biological community. Autotrophic respiration is divided into maintenance respiration and growth respiration. In addition to temperature, maintenance respiration is a function of the N content of living plant pools, and growth respiration is a fixed ratio of GPP (Hidy et al. 2016). The phenological module calculates foliage development. There are two models in the phenology module: the optional HSGSI method described in Hidy et al. 2012 and the original Biome-BGC model logic. In this study, we chose the original Biome-BGC model logic since our ecosystem type is forest. The soil flux module describes the decomposition of dead plant material and soil carbon pools. There are three significant developments of the soil flux module in the current model version: standing dead biomass and harvested biomass pools and a ten-layer soil sub-model.

Biome-BGCMuSo uses at least four input files when it is executed: initialization file (INI file), meteorological data file (MET file), soil property file (SOIL file), and a file for ecophysiological constants (EPC file) (Hidy et al. 2021). We elaborated the input files according to the particularity of the observation sites. For the INI file, CO₂ and nitrogen deposition are mainly set. The MET file includes the daily values of maximum and minimum air temperatures, precipitation, solar radiation, and vapor pressure deficit. In the SOIL file, we mainly set the soil texture parameters. The EPC file needs to be parameterized according to different PFTs. The detailed data sources and parameterization scheme are described in Section 2.3.

The model simulation is divided into two stages. The first is spinup simulation, which starts with very low initial levels of soil C and N and runs until it reaches a steady state under a given climate to estimate
the initial values of state variables (Thornton and Rosenbloom 2005). Next is the normal simulation, which uses the spinup simulations as the initial values of the C and N pools, and the simulation is performed within a predetermined period. Therefore, it is necessary to obtain a long-term series of daily data to drive the whole simulation. In this study, each simulation ran for 36 years from 1975 to 2010, with the first 28 years used as spin-up to bring the model into equilibrium and the last 8 years used for normal running.

2.3. Input data and parameterization

CO$_2$ concentration data were derived from the Mauna Loa CO$_2$ dataset and historical CO$_2$ dataset (http://www.co2.earth). N deposition was provided by ChinaFLUX (http://rs.cern.ac.cn). The soil texture dataset was provided by the Data Center for Resources and Environmental Sciences, Chinese Academy of Sciences (RESDC) (http://www.resdc.cn). The soil texture data were compiled based on the 1:1 million soil type map and the soil profile data obtained from the second soil survey in China. The soil texture was classified according to the percentage of sand, silt, and clay.

Meteorological data included daily minimum and maximum temperatures, the average daily air temperature, daily precipitation, daily average global radiation, and daily average water vapor pressure difference (VPD). First, we obtained the daily minimum temperature, daily maximum temperature and daily precipitation data from 1982 to 2003 for the four meteorological stations named Changbai (128°11′E, 41°25′N), Jiuji (101°29′E, 33°26′N), Xunwu (115°39′E, 24°57′N), and Fogang (113°32′E, 23°52′N) from the China Meteorological Data Network (http://data.cma.cn). These four meteorological stations are close to CBS, HB, QYZ, and DHS. Then, the meteorological station data were converted into the model input meteorological data of the corresponding flux station in the MT-CLIM 4.3 program for the spinup simulation. Finally, the model input meteorological data from 2003 to 2010 were obtained from ChinaFLUX and used for the normal simulation.

A total of 48 parameters in the EPC input file were selected to fluctuate within specific ranges according to the literature. First, basic values were determined by measurements and literature. Then, the variation range of each selected parameter fluctuated by 20% (White et al. 2000). Because of the individual biochemical and physical constraints, the maximum and minimum values of some parameters constitute the variation ranges. Table 2 shows the candidate input parameters selected in this study and their description information. The basic values and their source information of input parameters for CBS, HB, QYZ and DHS are shown in the Supplementary.

<table>
<thead>
<tr>
<th>Number</th>
<th>Parameter</th>
<th>Description</th>
<th>Unit</th>
<th>Varies with PFTs?</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>TGP</td>
<td>transfer growth period as a fraction of the growing season</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>2.</td>
<td>LGS</td>
<td>litterfall as a fraction of the growing season</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>3.</td>
<td>LFRT</td>
<td>annual leaf and fine root turnover fraction</td>
<td>1/year</td>
<td>Yes</td>
</tr>
<tr>
<td>4.</td>
<td>LWT</td>
<td>annual live wood turnover fraction</td>
<td>1/year</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Unit</td>
<td>Yes/No</td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>------------------------------------------------------</td>
<td>--------------------------------</td>
<td>--------</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td>WPM</td>
<td>whole-plant mortality parameter for the vegetation period</td>
<td>1/vegetation period</td>
<td>Yes</td>
</tr>
<tr>
<td>6.</td>
<td>C:N&lt;sub&gt;leaf&lt;/sub&gt;</td>
<td>C:N of leaves</td>
<td>kg C/kg N</td>
<td>Yes</td>
</tr>
<tr>
<td>7.</td>
<td>C:N&lt;sub&gt;lit&lt;/sub&gt;</td>
<td>C:N of leaf litter</td>
<td>kg C/kg N</td>
<td>Yes</td>
</tr>
<tr>
<td>8.</td>
<td>C:N&lt;sub&gt;fr&lt;/sub&gt;</td>
<td>C:N of fine roots</td>
<td>kg C/kg N</td>
<td>Yes</td>
</tr>
<tr>
<td>9.</td>
<td>C:N&lt;sub&gt;f&lt;/sub&gt;</td>
<td>C:N of fruit</td>
<td>kg C/kg N</td>
<td>Yes</td>
</tr>
<tr>
<td>10.</td>
<td>C:N&lt;sub&gt;lw&lt;/sub&gt;</td>
<td>C:N of live wood</td>
<td>kg C/kg N</td>
<td>Yes</td>
</tr>
<tr>
<td>11.</td>
<td>C:N&lt;sub&gt;dw&lt;/sub&gt;</td>
<td>C:N of dead wood</td>
<td>kg C/kg N</td>
<td>Yes</td>
</tr>
<tr>
<td>12.</td>
<td>DMC&lt;sub&gt;leaf&lt;/sub&gt;</td>
<td>dry matter content of leaves</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>13.</td>
<td>DMC&lt;sub&gt;lit&lt;/sub&gt;</td>
<td>dry matter content of leaf litter</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>14.</td>
<td>DMC&lt;sub&gt;fr&lt;/sub&gt;</td>
<td>dry matter content of fine roots</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>15.</td>
<td>DMC&lt;sub&gt;f&lt;/sub&gt;</td>
<td>dry matter content of fruit</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>16.</td>
<td>DMC&lt;sub&gt;s&lt;/sub&gt;</td>
<td>dry matter content of the soft stem</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>17.</td>
<td>DMC&lt;sub&gt;lw&lt;/sub&gt;</td>
<td>dry matter content of live wood</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>18.</td>
<td>DMC&lt;sub&gt;dw&lt;/sub&gt;</td>
<td>dry matter content of dead wood</td>
<td>kg C/kg DM</td>
<td>Yes</td>
</tr>
<tr>
<td>19.</td>
<td>L&lt;sub&gt;lab&lt;/sub&gt;</td>
<td>leaf litter labile proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>20.</td>
<td>L&lt;sub&gt;cel&lt;/sub&gt;</td>
<td>leaf litter cellulose proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>21.</td>
<td>FR&lt;sub&gt;lab&lt;/sub&gt;</td>
<td>fine root labile proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>22.</td>
<td>FR&lt;sub&gt;cel&lt;/sub&gt;</td>
<td>fine root cellulose proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>23.</td>
<td>F&lt;sub&gt;lab&lt;/sub&gt;</td>
<td>fruit labile proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>24.</td>
<td>F&lt;sub&gt;cel&lt;/sub&gt;</td>
<td>fruit cellulose proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>25.</td>
<td>DW&lt;sub&gt;cel&lt;/sub&gt;</td>
<td>dead wood cellulose proportion</td>
<td>Prop.</td>
<td>Yes</td>
</tr>
<tr>
<td>26.</td>
<td>W&lt;sub&gt;int&lt;/sub&gt;</td>
<td>canopy water interception</td>
<td>1/LAI/d</td>
<td>Yes</td>
</tr>
<tr>
<td>27.</td>
<td>k</td>
<td>canopy light extinction coefficient</td>
<td>DIM</td>
<td>Yes</td>
</tr>
<tr>
<td>28.</td>
<td>FLNR</td>
<td>fraction of leaf N in Rubisco</td>
<td>DIM</td>
<td>Yes</td>
</tr>
<tr>
<td>29.</td>
<td>g&lt;sub&gt;max&lt;/sub&gt;</td>
<td>maximum stomatal conductance</td>
<td>m/s</td>
<td>Yes</td>
</tr>
<tr>
<td>30.</td>
<td>g&lt;sub&gt;st&lt;/sub&gt;</td>
<td>boundary layer conductance</td>
<td>m/s</td>
<td>Yes</td>
</tr>
<tr>
<td>31.</td>
<td>SW</td>
<td>stem weight corresponding to maximum height</td>
<td>kg C</td>
<td>Yes</td>
</tr>
<tr>
<td>32.</td>
<td>R&lt;sub&gt;stmax&lt;/sub&gt;</td>
<td>maximum depth of the rooting zone</td>
<td>m</td>
<td>Yes</td>
</tr>
<tr>
<td>33.</td>
<td>GR</td>
<td>growth resp. per unit of C grown</td>
<td>Prop.</td>
<td>No</td>
</tr>
<tr>
<td>34.</td>
<td>MR&lt;sub&gt;perm&lt;/sub&gt;</td>
<td>maintenance respiration in kg C/day per kg of tissue N</td>
<td>kg C/kg N/d</td>
<td>No</td>
</tr>
<tr>
<td>35.</td>
<td>NSC:SC&lt;sub&gt;max&lt;/sub&gt;</td>
<td>theoretical maximum prop. of nonstructural and structural carbohydrates</td>
<td>DIM</td>
<td>No</td>
</tr>
</tbody>
</table>
2.4 Sensitivity analysis

Regression analysis and extended Fourier amplitude sensitivity testing (EFAST) were adapted for the sensitivity analysis of Biome-BGC MuSo, and the contributions of the input parameters to GPP and NPP were quantified. Details of the regression analysis and EFAST methods are provided in subsequent sections.

2.4.1 Sensitivity analysis based on regression analysis

The basic idea of regression sensitivity analysis is to obtain information about output sensitivity from the statistical analysis of the input data set generated by Monte Carlo simulation (Zagayevskiy and Deutsch 2015). Regression analysis derives the sensitivity measure as a parameter of the regression analysis applied...
to the input/output sample set (Hosman et al. 2010; Richard and Christopher 2020). Here, the multiple linear regression method was used to obtain the sensitivity to all single input factors at once. Since the input parameters have different units, the standard regression coefficient is used. The linear least squares estimation of regression coefficients is a measure of sensitivity, and the formula is expressed as

\[ SI_i = b_i \frac{SD(X_i)}{SD(Y)} \]  

(1)

where \( SI_i \) is the sensitivity of the i-th input parameter, \( b_i \) is the regression coefficient, \( SD(X_i) \) is the standard deviation of multiple sampling of the i-th input parameter, and \( SD(Y) \) is the standard deviation of the model's corresponding output Y (NPP and GPP).

2.4.2 Variance-based sensitivity analysis: EFAST

EFAST is a global sensitivity analysis algorithm that quantifies the sensitivity of a single parameter and multiple parameters to the outputs (Norton 2015). It is widely used in the sensitivity analysis of nonlinear models, such as Biome-BGC (Yan et al. 2016), crop growth models (Vazquez-Cruz et al. 2014), and building energy models (Nguyen and Reiter 2015). Each input parameter \( X_i \) has a range of random variables that results in the distribution of an output simulator \( Y \), which can be represented mathematically as

\[ Y = f(X) = f(X_1, X_2, ..., X_i, ..., X_n) \]  

(2)

where \( Y \) is the output (GPP and NPP) of Biome-BGCMuSo. \( X \) represents the set of input parameters, and \( X_i \) is the input parameter with a given upper and lower floating boundary.

EFAST indicates that the variance of the model output can adequately express the uncertainty of the parameter variations in the model results, as shown in equations (3)-(6):

\[ V_Y = \Sigma_i V_i + \Sigma_i \Sigma_{j>i} V_{ij} + \Sigma_i \Sigma_{j>i} \Sigma_{k>j} V_{ijk} + \ldots + V_{1,2,\ldots,n} \]  

(3)

\[ V_i = V[E(Y|X_i = x_i^*)] \]  

(4)

\[ V_{ij} = V[E(Y|X_i = x_i^*, X_j = x_j^*)] - V_i - V_j \]  

(5)

\[ V_{ijk} = V[E(Y|X_i = x_i^*, X_j = x_j^*, X_k = x_k^*)] - V_i - V_j - V_k \]  

(6)

where \( V_Y \) is the total variance of the model output, and \( V_i \) is the variance of the conditional expectation (VCE) of Y given that the i-th input \( X_i \) has a fixed value \( x_i^* \). \( V_{ij} \) is the VCE of Y given that the i-th input \( X_i \) has a fixed value \( x_i^* \) and the j-th input \( X_j \) has a fixed value \( x_j^* \). \( V_{ijk} \) is the VCE of Y given that the inputs \( X_i, X_j, \) and \( X_k \) have fixed values of \( x_i^*, x_j^*, \) and \( x_k^* \), respectively.

Sensitivity is measured by the contribution of a given input factor to the output variance (Pianosi et al. 2016). In this study, we selected the first-order sensitivity index \( (S_i) \) and the total sensitivity index \( (S_{IT}) \) to quantify the contributions of the input parameters to the outputs.

The first-order sensitivity index \( (S_i) \) measures the direct contribution of each input factor to the output variance or the expected reduction in output variance when a specific input is fixed. It can be represented mathematically as

\[ SI_i = b_i \frac{SD(X_i)}{SD(Y)} \]  

(1)

where \( SI_i \) is the sensitivity of the i-th input parameter, \( b_i \) is the regression coefficient, \( SD(X_i) \) is the standard deviation of multiple sampling of the i-th input parameter, and \( SD(Y) \) is the standard deviation of the model's corresponding output Y (NPP and GPP).
The total sensitivity index ($S_{IT}$) can be represented mathematically as

$$S_{IT} = 1 - \frac{\nu_x \mathbb{E}[y|x=x^*]}{\nu_y}$$  

In this study, 48 input parameters of Biome-BGCMuSo were evaluated by computing $SI_i$, $S_i$ and $S_{IT}$ for the GPP and NPP model outputs. First, according to the range of each input parameter (see Supplementary), the Monte Carlo method was used to uniformly sample each parameter. In this study, the sampling frequency was 4800 (48*100) for each forest PFT. Since CBS and DHS are mixed forests, the total sampling frequency of different PFTs at the 4 observation sites was 28800 (6*4800). According to the generated multiple sets of input parameters, we ran the Biome-BGCMuSo model in batches. GPP and NPP at the observation site from 2003 to 2010 were simulated for the normal stage. Second, the average GPP and NPP were calculated as the final model outputs. The sensitivity results using regression analysis and EFAST were analyzed in the RBBGCMuSo-master R package and SimLab 2.2. Finally, the sensitivity index ($SI_i$, $S_i$ and $S_{IT}$) was divided into two groups. When the sensitivity index is greater than 0.1, the corresponding parameter is the sensitive parameter; otherwise, the parameter is not the sensitive parameter.

In addition, the key sensitivity parameter refers to the corresponding parameter when $SI_i$ and $S_{IT}$ are both greater than 0.1.

### 3. Results

#### 3.1. Uncertainty in simulated GPP and NPP

The uncertainty of GPP and NPP from the input data was calculated using EFAST. Figure 2 shows the distribution of GPP. Generally, the GPP value of subtropical forests (QYZ and DHS sites) was higher than that of other forest sites. The GPP distribution of shrubs was relatively scattered, while that of ENF was relatively concentrated. QYZ with planted ENF and DHS with EBF had obvious discrete values. Table 3 shows the statistical data of the annual average GPP for forest PFTs at the observation sites. The uncertainty (coefficient of variation, CV) of GPP in DBF was greater than that in ENF. The CV of DBF at CBS was 39%, with a range of 168-1383 g C/m²/a for GPP. The uncertainty of ENF at CBS was 9%, with a range of 1417-2641 g C/m²/a for GPP. The uncertainty of GPP in planted forests was higher than that in natural forests, and the CVs of ENF at QYZ and DHS were 11% and 4%, respectively. In general, the uncertainty of temperate forest sites was higher than that in other climatic zones.

As shown in Figure 3, ENF at the CBS site had the highest NPP. The QYZ forest site with planted ENF had the most discrete NPP. The highest NPP uncertainty occurred in the DBF type (with CV=41%), which was similar to GPP (Tables 3 and 4).

Both GPP and NPP for ENF at the QYZ forest site had obvious discrete values. The amounts of GPP and NPP distributed in the ranges of 1842-3200 g C/m²/a and 200-400 g C/m²/a were zero, respectively. These findings illustrated that under certain parameter combinations, forests experience unsustainable or disturbed growth during years of model simulation. However, the sensitivity analysis was not affected by...
the above conditions due to the available and useful spinup phase, and it also explained that the sensitive parameters led to the scattered distribution of GPP and NPP values.

Figure 2 The distribution of the annual average GPP for forest PFTs at the observation sites

Table 3 The statistical table of the annual average GPP for forest PFTs at the observation sites

<table>
<thead>
<tr>
<th>Statistics</th>
<th>CBS</th>
<th>HB</th>
<th>QYZ</th>
<th>DHS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DBF</td>
<td>ENF</td>
<td>SHRUB</td>
<td>ENF</td>
</tr>
<tr>
<td>Min.</td>
<td>168</td>
<td>1417</td>
<td>1236</td>
<td>1842</td>
</tr>
<tr>
<td>Max.</td>
<td>1383</td>
<td>2641</td>
<td>2818</td>
<td>4471</td>
</tr>
<tr>
<td>Mean</td>
<td>617.6</td>
<td>2180.96</td>
<td>1863.43</td>
<td>4013.35</td>
</tr>
<tr>
<td>SD</td>
<td>238.28</td>
<td>189.54</td>
<td>294.45</td>
<td>455.54</td>
</tr>
<tr>
<td>CV (%)</td>
<td>39</td>
<td>9</td>
<td>16</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure 3 The frequency distribution histogram of the annual average NPP for forest PFTs at the observation sites

Table 4 The statistical table of the annual average NPP for forest PFTs at the observation sites

<table>
<thead>
<tr>
<th>Statistics</th>
<th>CBS</th>
<th>HB</th>
<th>QYZ</th>
<th>DHS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DBF</td>
<td>ENF</td>
<td>SHRUB</td>
<td>ENF</td>
</tr>
<tr>
<td>Min.</td>
<td>83</td>
<td>648</td>
<td>403</td>
<td>163</td>
</tr>
<tr>
<td>Max.</td>
<td>823</td>
<td>1318</td>
<td>1115</td>
<td>1088</td>
</tr>
<tr>
<td>Mean</td>
<td>352.12</td>
<td>1044.90</td>
<td>695.64</td>
<td>669.45</td>
</tr>
<tr>
<td>SD</td>
<td>143.75</td>
<td>109.47</td>
<td>125.28</td>
<td>146.08</td>
</tr>
<tr>
<td>CV (%)</td>
<td>41</td>
<td>10</td>
<td>18</td>
<td>22</td>
</tr>
</tbody>
</table>

3.2. Sensitivity analysis of GPP and NPP based on regression analysis

As mentioned in 2.4.2, sensitive parameters were those with \( SI_i \) greater than 10%. Figures 4(a) and 4(b) show the sensitive parameters of GPP and NPP calculated by regression analysis.

Overall, both GPP and NPP were sensitive to 8 parameters: \( C:N_{\text{leaf}} \), \( W_{\text{int}} \), \( k \), \( \text{FLNR} \), \( \text{GR} \), \( \text{MR}_{\text{pern}} \), \( \text{VPD}_f \), and \( \text{SLA}_1 \). Specifically, \( \text{MR}_{\text{pern}} \) was the parameter with maximum sensitivity for ENF and EBF types, especially in subtropical climate zones. At the shrub site, both GPP and NPP were sensitive to \( W_{\text{int}} \) and \( \text{SLA}_1 \), which was completely different from the other forest sites. Notably, one major difference in the sensitive parameters between GPP and NPP was \( C:N_{\text{fr}} \), that is, NPPs for all observation sites were not sensitive to \( C:N_{\text{fr}} \).

The sensitive parameters varied with different climatic zones. In temperate zone, \( \text{FLNR} \) was the common sensitive parameter for DBF and ENF, with respective \( SI_i \) values of 15.8% and 28.88% for GPP and 14.3% and 30.5% for NPP. In the alpine zone, GPP and NPP were severely restricted by \( W_{\text{int}} \). This may be because \( W_{\text{int}} \) controls the percentage of precipitation that enters the soil water pool and that is
transpired, while HB had the lowest precipitation among the four observation sites, and $W_{\text{int}}$ in turn became the main limiting factor in those water-stressed regions. In the subtropical zone, different PFTs also showed similar sensitive parameter combinations. C:N$_{\text{leaf}}$ exerted a significant control on GPP and NPP for all PFTs except the most sensitive parameter MR$_{\text{perm}}$. C:N$_{\text{leaf}}$ directly affects the distribution of carbon and nitrogen in leaves and then affects photosynthesis and cumulative productivity.

For different PFTs, individual parameters had a large impact on specific PFTs. Shrubs were most sensitive to $W_{\text{int}}$ (GPP: 38%; NPP: 38.7%) and SLA1 (GPP: 31.9%; NPP: 31.2%). For the evergreen types, MR$_{\text{perm}}$ was the most sensitive parameter, which mainly controlled plant growth. For DBF, VPD$_{f}$ exhibited very high sensitivity, with 50.4% and 49.7% for GPP and NPP, respectively.

![Figure 4](image)

**Figure 4** The $S_i$ of GPP (a) and NPP (b) at the observation sites

**3.3. EFAST for GPP and NPP**

The first-order sensitivity index ($S_i$) and total sensitivity index ($S_{iT}$) of the selected parameters for GPP and NPP at the four observation sites are shown in Figure 5 and Figure 6. Sensitive parameters were shown above the red dashed line.

As shown in Figure 5 and Figure 6, $S_i$ and $S_{iT}$ of VPD$_{f}$, $W_{\text{int}}$, SLA1, and $k$ were similar for GPP and NPP, which controlled GPP and NPP either directly or through interaction. FLNR was the common sensitive parameter in the temperate zone (CBS site). DBF and ENF at CBS site were most influenced by VPD$_{f}$ and $W_{\text{int}}$, respectively. For the unique shrub site, SLA1 was the most sensitive parameter for GPP. $k$ displayed the highest $S_i$ and $S_{iT}$ in subtropical zones (QYZ and DHS sites). MR$_{\text{perm}}$ exerted a significant control on NPP for all PFTs except shrubs. More sensitive parameters appeared in the total sensitivity index than those in $S_i$ for the QYZ and DHS sites. This indicated that numerous parameters strongly influenced GPP only through interactions.
Figure 5 EFAST sensitivity analysis results of GPP at the observation sites

Figure 6 EFAST sensitivity analysis results of NPP for forest PFTs at the observation sites

3.4. Comparison and analysis of the results for the two sensitivity analysis methods
Seven key sensitive parameters for GPP and NPP were summarized from the two sensitivity analysis methods: C:N$_{\text{leaf}}$, W$_{\text{int}}$, k, FLNR, MR$_{\text{pern}}$, VPD$_{f}$, and SLA1 (Figure 7 and Figure 8). The sensitive parameters selected by regression analysis were similar to those from EFAST, and the key sensitive parameters differed significantly under various climate environments and PFTs. FLNR was the key sensitive parameter in temperate zone, and C:N$_{\text{leaf}}$ was the key sensitive parameter in subtropical zones. VPD$_{f}$ was the key sensitive parameter for DBF, and GR was the key sensitive parameter for ENF at the CBS site. At the DHS site, C:N$_{\text{leaf}}$ and k were the key sensitive parameters of EBF, and C:N$_{fr}$ was the key sensitivity parameter of ENF. In addition, C:N$_{fr}$ was the sensitive parameter only for ENF-type GPP at the DHS site, while GR was the sensitive parameter only for ENF-type NPP at the CBS site.

**Figure 7** The key sensitivity parameters of GPP for different forest PFTs at the observation sites

**Figure 8** The key sensitivity parameters of NPP for different forest PFTs at the observation sites
4. Discussion

4.1. A framework for optimizing forest primary productivity parameters based on sensitivity analysis

The key sensitive parameters extracted according to different sensitivity analysis methods have a high degree of similarity. It is therefore necessary to perform a series of steps for key sensitivity parameters to simplify the process from sensitivity analysis to parameter correction. Here, we refer to these steps as the "workflow". The workflow for the application of key parameters is shown in Figure 9. The colored parameters should be of importance in sensitivity analysis and modeling. We described and discussed the workflow and the choices that the user must make in each step to provide practical guidelines to support the user in the sensitivity analysis-based simulation correction of the parameters.

The most important thing in the experimental design of sensitivity analysis is to determine the parameters and sensitivity analysis methods. These together constitute what we call the "experimental settings." Specifically, the chosen parameters include (i) selecting the input factors to be accepted by the sensitivity analysis and their floating intervals and (ii) setting the values of other input factors, and these input factors will remain constant throughout the sensitivity analysis. The selection of sensitivity analysis methods can be found in the application process of sensitivity analysis proposed by Pianosia et al. (2016).

The results described in sections 3.2 and 3.3 indicate that the sensitivity of the climate environment to productivity simulation is greater than the difference in PFTs. Specifically, the most common sensitivity parameter of different PFTs in the temperate zone was FLNR, followed by MR_{per}. In the alpine zone, the common sensitive parameters of different PFTs were SLA1 and W_{int}. In addition, C:N_{leaf} was the key sensitive parameter for different PFTs in the subtropical zone, followed by MR_{per}. Next was the selection of key sensitive parameters for different PFTs. In the temperate zone, DBF was sensitive to VPD_{f}, and ENF was sensitive to GR. In the subtropical zone, EBF was sensitive to k, and ENF was sensitive to C:N_{fr}. In addition, GR and C:N_{fr} were the key sensitive parameters of NPP and GPP, respectively, excluding the common key sensitive parameters of NPP and GPP. As the importance of the parameters gradually decreases with the deepening of the workflow, the disturbance effect of the following parameters on the simulation results gradually decreases. In the application workflow for key parameters, if some key sensitive parameters (such as GR and C:N_{fr}) have been added before, the corresponding steps can be omitted in the following process.

The uncertainty discussed in Section 3.1 is intended to assess the uncertainty of the results of a particular sensitivity analysis method, therefore providing information on the reliability of the results within the scope of the method. A different and equally relevant question is the degree to which the method itself can be trusted, that is, whether the method is suitable for solving the expected answer when applied to the immediate question. For example, variance-based sensitivity analysis methods rely on the assumption that variance is a wise substitute for uncertainty and may not be correct for highly skewed output distributions. In this case, even if researchers can obtain an almost completely accurate estimate of the sensitivity index based on variance, they cannot provide a correct ranking (Liu et al. 2005). Therefore, the sensitivity analysis results may be very reliable, but they still need to be based on actual conditions.
Circumstances evaluate the accuracy of the results and explain the reasonableness of the sensitivity analysis results.

Figure 9 A framework for optimizing forest primary productivity parameters based on sensitivity analysis

4.2. Uncertainty of the input parameters

The use of the input parameter values of a specific site can achieve the best simulation and a relatively high degree of acceptance of the sensitivity analysis results (Thornton et al. 2002; Toriyama et al. 2021). There are two main limitations: (1) Some input parameters cannot be directly observed, such as FLNR and parameters related to decomposition and distribution (L_{lab}, L_{cel}). (2) The variation range of parameters is difficult to obtain. In this study, the main parameters related to C and N allocation, plant height, and root depth were obtained from actual measurements or research at the observation sites. Parameter localization was carried out based on the model default parameters (see Supplementary).

To explore the impacts of different basic values of the parameters on outputs, we analyzed the simulated GPP of the CBS site under three schemes: (1) default parameters; (2) localized parameters; and (3) corrected parameters based on sensitivity analysis. The results were validated against EC measurements, as shown in Figure 10. Rows (a), (b) and (c) represent different PFTs of the mixed forest, DBF and ENF, respectively. The results show that the model calibrated by sensitivity analysis had the best simulation compared with EC measurements, especially for ENF, with $R^2 = 0.69$, which improved by 16% and 10% compared to schemes 1 and 2. The sensitive parameters control the key processes associated with the GPP simulation. By correcting related sensitive parameters, the uncertainty of input parameters can be effectively reduced, and the simulation accuracy of the process model can be improved.
Figure 10 Correlation analysis of simulated GPP and vorticity flux observation values under three parameterization schemes at the CBS site

Previous studies showed that parameters with smaller basic values were more susceptible to the influence of the parameter range, and a narrow range would limit the sensitivity index of a small parameter (Ma et al. 2020). Therefore, the range of the parameter is crucial to the result of the sensitivity analysis. In this study, under the premise of giving priority to physical or biological constraints, the localized parameters are all taken as the parameter perturbation range with fluctuations of 20% (White et al. 2000). The consistency of the parameter range is guaranteed to a certain extent.

4.3. Sensitive parameters

According to recent studies, it was predicted that forest carbon sequestration decreased with increasing carbon dioxide and would possibly be a carbon source in the future (Cox et al. 2000; Baccini et al. 2017; Brienen et al. 2020). In contrast, some studies demonstrated that the absorption capacity of forest carbon sinks would continue (Wang et al. 2020; Harris et al. 2021; Heinrich et al. 2021). This means that considerable uncertainties exist during carbon flux simulation and even the climate-forest carbon cycle feedback mechanism. Therefore, sensitivity analysis was applied in this study, aiming to distinguish the model’s influential parameters and examine carbon flux output sensitivity.

Our results showed that 7 parameters had important impacts on both GPP and NPP. However, many parameters in BIOME-BGCMuSo exhibited extremely low sensitivity for GPP and NPP, for example,
LGS (litterfall as a fraction of the growing season), LWT (annual live wood turnover fraction), and parameters related to the dry matter content (DMC_{lit} (dry matter content of leaf litter), DMC_{f} (dry matter content of fruit), and DMC_{dw} (dry matter content of dead wood)). The parameters that most influenced GPP and NPP were those controlling respiration and the assimilation rate of photosynthesis, such as MR_{pern}, FLNR, and C:N_{leaf}. This result is consistent with the results from White (2000), Raj (2014), and Dagon (2020). MR_{pern} represents the maintenance respiration in kg C/day per kg of tissue N, which is directly related to maintenance respiration and further affects GPP and NPP (Ryan 1991). FLNR controls the potential rate of carboxylation and directly affects V_{C_{max}}; therefore, it is a dominant control of canopy assimilation (White et al. 2000; Stitt and Schulze 1994). C:N_{leaf} is a compound parameter that determines the important factors of the nitrogen required to construct leaves, the amount of nitrogen available for investment in photosynthetic machinery, and leaf respiration rates.

The sensitive parameters varied under different climate and environmental conditions. FLNR had a strong influence on GPP and NPP in the temperate zone; C:N_{leaf} was sensitive in the subtropical zone. This indicated the limiting effects of light, water, temperature and mineral nutrients on primary productivity under different climatic environments in previous studies (Knapp et al. 2014). In addition, many studies have shown that leaf traits change significantly along temperature and rainfall gradients (Domínguez et al. 2012; Wright et al. 2017). As the latitude increases, Rubisco activity is significantly inhibited, which affects FLNR and inhibits the assimilation of C. In contrast, the temperature weakly restricts the activity of Rubisco in subtropical areas. This may explain why FLNR has high sensitivity in the temperate zone. C:N_{leaf} is directly related to the nitrogen content in the leaves. The nitrogen content directly affects the content of chlorophyll, thereby affecting photosynthesis. Gong et al. (2020) investigated the leaf traits of different life forms at different latitudes in northeastern China and found that nitrogen was limited in low latitude areas and that leaf traits were very sensitive to climate factors. Our results clarify the key sensitivity parameters of GPP and NPP in different climatic environments and provide information for the accurate simulation and parameter correction of GPP and NPP at regional scale.

5. Conclusions

Two sensitivity analysis methods, regression analysis and EFAST, were used in this work to determine the key parameters of the Biome-BGCMuSo model. The key sensitivity parameters extracted according to different sensitivity analysis methods had a high degree of similarity. The results demonstrated that C:N_{leaf}, W_{int}, k, FLNR, MR_{pern}, VPD_{i}, and SLA1 were the most sensitive parameters for GPP and NPP. Specifically, GPP and NPP were most sensitive to FLNR, SLA1 and W_{int}, and C:N_{leaf} in temperate, alpine and subtropical zones, respectively. Finally, we suggested a framework of sensitivity analysis by considering different climate conditions, which would present a reliable solution of decreasing the complexity of calibrating process-based models. We emphasize that the calibration of parameters should be based on PFTs, and more attention should be paid to the differences in climate and environment.

Abbreviations

<table>
<thead>
<tr>
<th>Abbreviations</th>
<th>Description</th>
</tr>
</thead>
</table>
Note: The abbreviated representation and description of the model input parameters are shown in Table 2.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The datasets used or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests

Funding

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Authors' contributions

Hongge Ren and Li Zhang devised the main theoretical framework and proof outline. Hongge Ren performed the analytic calculations and model simulations and took the lead in writing the manuscript. Min Yan and Xin Tian provided significant feedback and helped shape the research, analysis and manuscript. Xingbo Zheng provided some of the climate data for the research. All authors read and approved the final manuscript.
Acknowledgments

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FAO (2020) Global Forest Resources Assessment 2020. FAO


Supplementary Files

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- Supplementary.pdf